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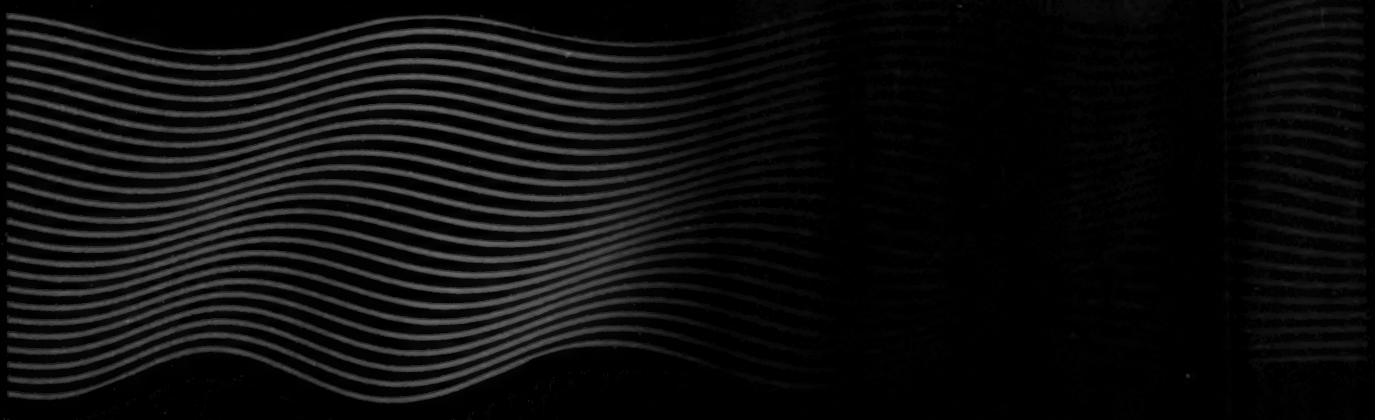
Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques



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EDITORIAL / ÉDITORIAL

Our first communication with CJFAS contributors and readers is to assure you that there will be no immediate or major changes in Journal policy or practice. We do expect, however, that there will be gradual changes in both. Instructions to Authors and NRC Research Press Publication Policy, which can be found in the first issue of each year, remain presently unchanged except for the address of our editorial offices. Some changes in reviewing procedures and advice to referees will follow, but there will certainly be no change in rigor of review. There are substantial changes in Associate Editors and the Editorial Board, whose roles are now combined. The expanded group of Associate Editors now more nearly reflects the national and international mix of authors and affiliations. We have enlisted the assistance and advice of active researchers who are leaders in their disciplines; the majority of them have substantial histories as reviewers for the journal.

We hope and intend to move progressively to electronic transmission of manuscripts between the editorial office, contributors, reviewers and associate editors. This will be done while maintaining full confidentiality and with the object of speeding the review process. Manuscripts will still also be accepted and transmitted by conventional means. A new "fast-track" publication process will also be initiated; please enquire by e-mail at

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for criteria and instructions.

We approach our duties as editors of CJFAS with a mixture of sentiments: apprehension towards our new responsibilities, pride in the reputation of the Journal, and security from the loyalty of its contributors and subscribers. There can indeed be few communities of scientists who exhibit such loyalty to "their Journal," despite the fact that it is not affiliated with any society. CJFAS has evolved steadily from its FRB roots to become truly interdisciplinary and international in scope. In part, this reflects the increasingly international character and relevance of ecological and socioeconomic concerns in aquatic environments, but in larger part, it reflects the scientific maturity and stature of the contributors to CJFAS. By any criterion, Canadian scientists constitute a major set of players in the international aquatics and fisheries community. The Journal's "Canadian" appellation is therefore no parochialism, but it still describes the affiliation of a majority of its contributors. In 1996, some 50% of contributions were from Canada (63% from universities, 32% from government, 5% others), 30% were from the USA, and the remaining 20% were from other countries. This mix has resulted largely by a process of natural selection, and it may have reached an approximate, perhaps appropriate, equilibrium. We see no need to engage in artificial selection.

Finally, we thank all of you who have already wished us well in our new duties and hope that we will prove worthy of your confidence and deserving of your continued support. Our thanks go especially to David Cook, who has been of major assistance during an almost painless transition period. We

Dans cette première communication avec nos lecteurs et collaborateurs, nous voulons insister sur le fait que les politiques et l'orientation du Journal ne subiront aucune modification immédiate ou radicale. Les changements que nous y apporterons seront plutôt graduels et bénins. Les recommandations aux auteurs et la politique des Presses scientifiques que vous retrouvez dans le premier numéro de chaque année restent les mêmes et seule notre adresse a changé. Vous verrez plus tard un certain remaniement des modalités d'arbitrage et des recommandations aux réviseurs, mais l'examen par les pairs se fera toujours avec la même rigueur. Le groupe des directeurs scientifiques associés et du Comité de rédaction seront transformés en raison du regroupement de leurs rôles. Le nouveau groupe de directeurs scientifiques associés traduit mieux l'amalgame national et international des auteurs et des affiliations. Nous nous sommes adjoint l'aide de chercheurs reconnus qui sont des chefs de file dans leurs disciplines respectives. En outre, la plupart ont déjà fait leurs preuves en tant qu'examinateurs pour le Journal.

Un de nos buts est d'accélérer le processus d'examen en recourant à la transmission électronique, mais toujours confidentielle, des articles entre la Rédaction, les collaborateurs, les examinateurs et les directeurs scientifiques. Les auteurs auront quand même le loisir de soumettre leurs articles de la façon habituelle. Nous comptons mettre sur pied un processus accéléré de publication. Pour obtenir de plus amples renseignements sur les critères et les recommandations, envoyez un message électronique à cet effet à

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Divers sentiments nous animent avec notre arrivée en poste — une certaine crainte devant nos nouvelles fonctions, la fierté dans la réputation du Journal et la sécurité apportée par la fidélité de nos collaborateurs et abonnés. Rares sont les communautés scientifiques qui professent un attachement aussi profond envers ce qui est en fait «leur» Journal, et ce, même s'il n'est rattaché à aucune société savante. Le Journal a connu une évolution soutenue pour devenir la tribune internationale et multidisciplinaire que nous connaissons aujourd'hui. Cette transformation reflète d'une part la portée et la pertinence internationales des préoccupations écologiques et socio-économiques concernant les milieux aquatiques et d'autre part le calibre scientifiques de nos collaborateurs. Les scientifiques canadiens jouent un rôle déterminant dans les sciences halieutiques et aquatiques à l'échelle mondiale. Ce n'est pas par pur hasard que «canadien» se retrouve dans notre titre. En 1996, 50 % des articles étaient d'auteurs canadiens (universités, 63 %, gouvernements, 32 %, autres, 5 %), 30 % d'auteurs américains et 20 % d'auteurs d'autres pays. Cette répartition est le résultat d'une sélection naturelle qui mené à un équilibre à la fois approximatif et approprié. Nous ne voyons pas l'utilité ou la nécessité d'intervenir dans ce processus naturel.

Nous voulons remercier tous ceux qui nous ont fait part de leurs bons voeux. Nous espérons être à la hauteur de vos attentes et de votre confiance. Nous voulons surtout remercier David Cook qui a assuré une transition en douceur. Nous avons souvent fait

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have relied on him heavily for advice and suggestions in issues of continuity versus change in editorial practice. We also thank Aldyth Holmes and Bruce Dancik for their advice and confidence in us.

John C. Roff, Moira M. Ferguson
Editors/Directeurs scientifiques

appel à ses conseils et à ses suggestions lorsque l'orientation de la politique rédactionnelle était sous le microscope. Nous voulons également remercier Aldyth Holmes et Bruce Dancik pour leur confiance et leurs conseils de tous les instants.

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A functional classification of the drift: traits that influence invertebrate availability to salmonids

Russell B. Rader

Abstract: Twelve categories/traits were used to classify and rank aquatic invertebrates based on their propensity to drift and importance as a food resource for salmonids. Invertebrate availability was based on their (*i*) propensity to intentionally drift, (*ii*) likelihood of being accidentally dislodged by the current, (*iii*) drift distance, (*iv*) adult drift, (*v*) benthic exposure, (*vi*) body size, and (*vii*) abundance. This study represents the first attempt to characterize the intentional drift propensity of stream invertebrates. A ranking procedure separated invertebrates into *Baetis* and three groups decreasing in availability. Predicted ranks were significantly correlated with the actual rank of invertebrates in trout guts taken in three separate studies conducted in the central Rocky Mountains, suggesting that this procedure can effectively rank invertebrates based on their availability as a food resource for salmonids. A cluster analysis separated the 95 taxa into four drift guilds and six availability groups. This study provides criteria for determining when alterations in invertebrate community composition will affect food resources for higher trophic levels by causing a decline in the most available taxa. This research also supports previous findings that floods are important in maintaining invertebrates that represent an important food resource for salmonids.

Résumé : Douze catégories ou traits ont été utilisés pour classer les invertébrés aquatiques et leur attribuer un rang d'après leur tendance à dériver et leur importance comme ressource alimentaire pour les salmonidés. La disponibilité des invertébrés a été établie en fonction (*i*) de leur tendance à dériver intentionnellement, (*ii*) de la probabilité qu'ils soient emportés accidentellement par le courant, (*iii*) de la distance de dérive, (*iv*) de la dérive des adultes, (*v*) de l'exposition benthique, (*vi*) de leur visant à caractériser la tendance à dériver intentionnellement des invertébrés de cours d'eau. Une méthode d'attribution de rangs a servi à séparer les invertébrés en *Beatis* et trois groupes de disponibilité décroissante. Les rangs prévus étaient corrélés de manière statistiquement significative avec les rangs réels occupés par les invertébrés dans les estomacs de truite dans trois études distinctes réalisées dans la région centrale des montagnes Rocheuses, ce qui indiquerait que cette méthode peut effectivement servir à hiérarchiser les invertébrés en fonction de leur disponibilité comme ressource alimentaire pour les salmonidés. Une analyse par grappe a séparé les 95 taxons observés en quatre groupes de dérive et six groupes de disponibilité. Cette étude fournit des critères permettant de déterminer quand les modifications de la composition de la communauté des invertébrés influeront sur les ressources alimentaires des niveaux trophiques plus élevés en entraînant une réduction des taxons offrant la plus grande disponibilité. Ces travaux viennent également appuyer les constatations antérieures voulant que les inondations soient importantes pour maintenir les populations d'invertébrés qui représentent une ressource alimentaire importante pour les salmonidés.
[Traduit par la Rédaction]

Introduction

Invertebrates play an important role in lotic ecosystems by influencing functional processes (e.g., decomposition, primary production, nutrient spiraling) and by forming the major link between primary producers and higher trophic levels (fish). As a food resource, not all invertebrates are equally important. Differences in predator (e.g., trout versus sculpin) and prey (mayflies versus clams) traits (morphology, behavior, life history) create differences in availability. For example, most trout (the focus of this study) feed primarily in the drift, and some aquatic insects are only available in the drift as adults since immature stages occur in the hyporheic zone (DeWalt and Stewart 1995), are inactive during the summer (diapause), or are concealed within the epibenthic habitat (Ward 1992). The ecotrophic coefficient is the proportion of the total benthic invertebrate production that is consumed by the entire fish assemblage (Ricker 1946). In trout streams, this proportion likely ranges between 0.30 and 0.50 (Waters 1988). Such low ecotrophic coefficients (Waters 1988) can, in part, be explained by differences in availability among invertebrates. For salmonids, availability is primarily defined by the propensity to drift (both immature nymphs and adults). I propose a conceptual model and procedure for ranking invertebrates based on their availability to drift-feeding salmonids. Ranking aquatic invertebrates according to their importance in maintaining food supplies for higher trophic levels may be an important step in predicting the effects of disturbances (floods, dams, diversions, pollutants) on trout populations. If the impact of disturbances on highly ranked invertebrates is determined, changes in salmonid food resources can be predicted.

Classifying organisms into ecological aggregates that are functionally similar and transcend taxonomic boundaries (functional groups or guilds) is a valuable approach applied to a wide range of organisms for a variety of purposes (Southwood

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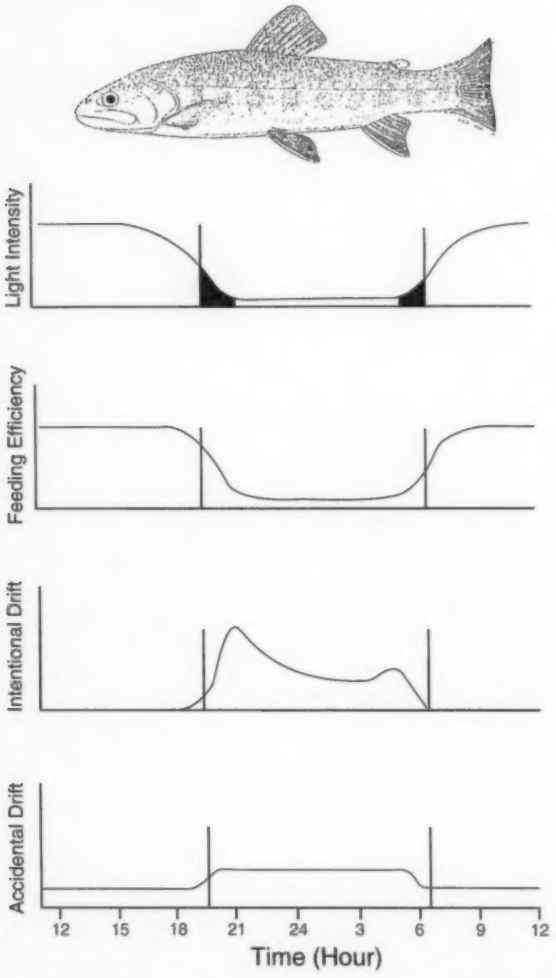
Fig. 1. Conceptual model showing the diel relationships between light intensity, trout feeding efficiency, and intentional and accidental drift of aquatic macroinvertebrates. Note that intentional drift is confined to periods of darkness (twilight and night). See text for a complete explanation.



1988; Keddy 1994). In streams, the guild or functional group concept has been successfully applied to invertebrates (Cummins 1973; Growns and Davis 1994; Merritt and Cummins 1995), fish (Karr et al. 1986; Poff and Allan 1995), and most of the plants and animals of an entire river ecosystem (Resh et al. 1994). One of the most appealing aspects of the guild concept is its ability to condense a large amount of species-specific information into a few categories that have generalized attributes, thus reducing the complexity associated with a large number of species (Hawkins and MacMahon 1989; Townsend and Hildrew 1994).

The objective of this paper is to provide criteria for classifying stream invertebrates into guilds based on their propensity to drift and to rank invertebrates based on their importance as a food resource for trout. I have estimated the dietary importance of various taxa in small to midsized snowmelt run-off streams of the subalpine, montane, and foothill zones of the central Rocky Mountains. The taxonomic categories used in this study were primarily taken from Ward and Kondratieff (1992). Taxa found in trout streams of the central Rocky Mountains were classified at the order, family, or genus level and ranked with respect to criteria that determine availability: (*i*) adult and immature drift propensity, (*ii*) exposure of taxa inhabiting the surface benthos, (*iii*) general patterns of relative abundance, and (*iv*) invertebrate body size.

Methods

Conceptual model

Figure 1 represents the conceptual basis for this paper and summarizes the following information. Trout are visual, size-selective, opportunistic generalists that primarily feed on the drift (e.g., Newman 1987; Allan 1995). Although benthic feeding is prevalent in turbid rivers (Tippets and Moyle 1978), among young-of-the-year (YOY) (Grant and Noakes 1987; Hubert and Rhodes 1992) and apparently among salmonids with a subterminal mouth (Nakano and Furukawa-Tanaka 1994), drift-feeding is the primary means of energy acquisition for most juvenile and adult salmonids in the Rocky Mountains and remains an important part of the diet for larger (>30 cm) piscivores (e.g., Griffith 1974; Angradi and Griffith 1990; Nakano et al. 1992). Prey detection and foraging efficiency are reduced with decreasing levels of light (Jenkins 1969; Ginetz and Larkin 1976; Hyatt 1979; Wilzbach et al. 1986). Invertebrates entrained in the drift during daylight hours and at twilight periods (dawn and dusk) are most easily detected and therefore most available to salmonids. Except for bright moonlit nights, night drift (before morning and after evening twilight) is primarily unavailable. Recent research provides convincing evidence that invertebrate nocturnal drift is an effective predator avoidance adaptation to minimize the risks of predation by drift-feeding fish (Allan 1978; Dill 1987; Flecker 1992; Douglas et al. 1994; McIntosh and Peckarsky 1996).

Stream invertebrates can be accidentally dislodged (passive drift) or, for various reasons, intentionally enter the drift (e.g., Peckarsky 1980; Kohler 1985; Malmqvist and Sjöström 1987; Forrester 1994; Scrimgeour et al. 1994). The term "intentional" implies an active process resulting from the decisions made by individuals (Dill 1987). Except for catastrophic drift induced by stressful conditions (stranding, oxygen deficiency), it appears that most intentional/active drift is primarily confined to hours of darkness when fish prey detection is reduced (Walton 1980; Ciborowski 1983; Kohler 1985; Rader and McArthur 1995; Wooster and Sih 1995), whereas most daytime drift is accidental or associated with changes in life cycle events (Waters 1965, 1972; Ciborowski 1983). Recent research has shown that trout can suppress daytime drift (e.g., Flecker 1992; Douglas et al. 1994; McIntosh and Peckarsky 1996) and that invertebrates will often delay drifting until night in response to unfavorable conditions initiated during the day (e.g., Poff and Ward 1991; Rader and McArthur 1995). Although the prevalence of intentional versus accidental drift during the night night versus the day requires further investigation, several studies suggest that most intentional drift is confined to the safer periods of darkness and the amount of intentional drift during the day is probably small compared with accidental dislodgment and drift associated with changes in life cycle events.

If there were no twilight periods (dusk and dawn), there would be no need to classify invertebrates based on their propensity to intentionally drift because invertebrates that intentionally leave the substrate probably confine their drifting activity to periods of darkness and are therefore relatively unavailable as food for salmonids. Even though salmonid feeding efficiency declines with decreasing irradiance (e.g., Wilzbach et al. 1986), several studies indicate that salmonids can actively feed at twilight (McCormack 1962; Ringler

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Table 1. Traits or categories and scores used to classify stream invertebrates based on their availability to drift-feeding salmonids.

Categories/scores	0	1	3	6	9
Intentional drift	No drift/catastrophic	Rare	Occasional	—	Frequent
Accidental drift					
Habitat	Hyporheic	Depositional	—	—	Erosional
Flow exposure	Avoiders/NA	Obligates	—	Facultatives	—
Mobility	Sessile/NA	Attached	Crawlers	—	Swimmers
Drag index	NA	<6.0	6.0–12.0	>12.0	—
Drift distance	Passive sinkers/NA	Active swimmers	Active settlers	Passive floaters	—
Adult drift					
Emergence behavior	Winter/NA	—	Crawl to bank	Drift/swim to surface	—
Ovipositing behavior	Overhanging vegetation/NA	—	Crawl underwater/dropped	Run across/land on surface	—
Diel activity	NA	Nocturnal	—	Diurnal	—
Benthic exposure	Buried/hyporheic	Concealed	Exposed	—	—
Size (mm)	—	<1.0	1.0–5.0/>20.0	—	5.1–20.0

Note: NA indicates subcategory scores for taxa when categories were not applicable. For example, the Flow Exposure category would not apply to taxa that spend most of their life cycle in the hyporheic zone. A dash indicates that no subcategory was assigned to that particular score.

1979; Bachman 1984; Clapp et al. 1990). Invertebrates that intentionally drift or are accidentally dislodged during twilight periods are exposed to predation and likely make a significant contribution to salmonid energy intake. Therefore, invertebrates were classified based on their propensity toward both accidental dislodgment (during the day and at twilight) and intentional drift (twilight).

Why would stream invertebrates intentionally drift at twilight if they are exposed to trout predation? Invertebrates that intentionally drift at twilight probably leave the safety of the substrate because of their inability to accurately detect levels of light in the water column. At twilight, invertebrates that inhabit substrate crevices are undoubtedly exposed to a darker microenvironment than the level of light surrounding salmonids. Holt and Waters (1967) suggested that the gradual increase in drift at dusk, rather than a sudden and synchronized rise, may be caused by the exposure of invertebrates to varying levels of light and amounts of shadow in the benthos. On a larger scale, invertebrates from dark, shaded stream sections may drift at twilight into brighter reaches with an open canopy. At twilight, many invertebrates may intentionally but prematurely drift from dark habitats into a dimly lit water column with a bright background sky, exposing themselves to predation by trout. Hence, understanding invertebrate availability to trout requires characterizing both accidental dislodgment and intentional drift propensity.

Ranking procedure

In addition to categories defining benthic exposure and size, nine categories ("Intentional Drift", "Habitat", "Flow Exposure", "Mobility", "Drag Index", "Drift Distance", "Emergence Behavior", "Ovipositing Behavior", and "Diel Activity") were used to classify stream invertebrates based on their propensity to intentionally drift, accidental dislodgment by the current, and the drift characteristics of adults (Table 1). All categories were divided into subcategories/species traits. Each invertebrate taxon was assigned to a single subcategory and received the corresponding score. The higher the score the greater the availability as a food resource for trout. Invertebrates were ranked based on their total score summed across all categories. The procedure used to assign invertebrates to specific subcategories had an ordered, hierarchical arrangement. Invertebrates were classified starting with the top category and proceeding down the table (Table 1). Habitat had an important influence on a taxon's total score or rank. For example, Flow Exposure, Mobility, Drag Index, and Drift Distance did not apply (NA) to taxa inhabiting the hyporheic zone or depositional areas. (I assumed that accidental dislodgment and drift entry from hyporheic and depositional areas was rare.) Similarly, Emergence Behavior and Oviposition Behavior did not apply to noninsect taxa.

Numerous publications (>50) on aquatic invertebrate biology were used to classify taxa (i.e., Claassen 1931; Needham et al. 1935; Ross 1944; Jensen 1966; Harper and Hynes 1972; Harper 1973; Wiggins 1973, 1996; Edmunds et al. 1976; Baumann et al. 1977; McAlpine et al. 1981; McCafferty 1981; Stewart and Stark 1984, 1988; Swisher and Richards 1991; Ward and Kondratieff 1992; DeWalt and Stewart 1995; Merritt and Cummins 1995). Information on some traits was often not known for all species in a taxonomic group. The traits used to characterize some genera were often based on information from a single "Type" or "Exemplar" species (as in Merritt and Cummins 1995). Also, some taxa were difficult to assign to a single subcategory. For example, most species in the families Nemouridae and Leuctridae are winter stoneflies but some species emerge in the summer (Harper 1973). When a genus contained species that could fit into more than one subcategory, the most prevalent subcategory was chosen. The taxonomic resolution (order, family, or genus) used in the classification process was determined by the redundancy of traits within a group. For example, all genera in the family Heptageniidae in trout streams of the Central Rocky Mountain region had the same traits and were classified in the same subcategories. I used two criteria to determine the level of taxonomic resolution. When one or more genera in a family occupied different habitats (hyporheic, depositional, or erosional) or occupied the same habitat but differed by two or more of the other 11 categories, the family was separated at the generic level. Habitat was important because it would determine the applicability (NA) of subsequent categories which could have a important influence on the magnitude of the final score.

Category descriptions

Intentional drift

Most stream invertebrates can *intentionally* enter the drift in an attempt to avoid extreme conditions that fluctuate beyond the normal range of variation (disturbance/catastrophic drift). For example, numerous invertebrate taxa intentionally drifted in response to oxygen stress when flow was reduced in a small (50 cm wide) cold-water spring in Idaho (Minshall and Winger 1968). I have attempted to identify invertebrates that under normal, nondisturbance conditions intentionally drift and are therefore consistently available for salmonid consumption (primarily at twilight). Under nondisturbance conditions, stream invertebrates probably range from frequent intentional drifters to taxa that rarely intentionally enter the drift. I make the assumption that there is a relationship between intentional drift propensity and the ability to exit the drift. The ability to efficiently exit the drift will determine the magnitude of the risks associated with

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drifting (e.g., time of exposure to salmonid predation) and, therefore, the intentional drift frequency. Data on drift distances of various taxa (Elliott 1971; Otto and Sjöström 1986; Allan and Feifarek 1989) and the behavioral responses of mayfly prey to stonefly predators support this assertion (Corkum 1978; Peckarsky 1980; Molles and Pietruszka 1983; Williams 1987; Peckarsky and Penton 1989). The ability to exit the drift depends on settling efficiency, and settling efficiency depends on three factors: (*i*) swimming ability, (*ii*) agility in regaining a foothold on the substrate (e.g., trailing a silk thread), and (*iii*) sinking postures. Stream invertebrates were classified according to these three criteria using information derived from a variety of sources on settling efficiency, drift distances, and behavioral observations (e.g., Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986; Williams 1987; Peckarsky and Penton 1989). I also reviewed the literature on intentional drift to gather empirical data on the intentional drift frequency of various taxa (Table 2). Based on this review, four nondisturbance mechanisms can elicit an intentional drift response: (*i*) avoidance of predators, (*ii*) avoidance of nonpredatory, aggressive interactions, (*iii*) searching for a patchily distributed food resource, and (*iv*) oxygen regulation. The intentional drift frequency (rare, occasional, and frequent) of specific taxa has only been determined for confrontations with predators and aggressors (Table 3). Taxa were classified as "Rare", "Occasional", and "Frequent" based on the percentage of encounters (predation or aggression) producing an intentional drift response (Frequent ≥ 50%; 50% < Occasional > 10%; Rare ≤ 10%). Taxa with apparently no propensity to intentionally drift except when stranded or otherwise physiologically stressed were placed in the "No Drift/Catastrophic" category. Since this review included only a small proportion of the invertebrate assemblage, a procedure that maximized empirical information from Table 3 was used for classifying most taxa without empirical data. Taxa with known settling traits but absent in the review (no empirical data) were given the same classification as taxa in Table 3 with the same settling traits (e.g., swimming ability, stone cases, drift posture, etc.). Taxa absent from the review with unknown settling traits were classified based on the intentional drift frequency or settling efficiency (e.g., Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986) of taxa present in Table 3 with the same mobility characteristics (sessile, attached, crawlers, swimmers).

An abundance of information indicated that *Baetis* were frequent intentional drifters (Table 3). Amphipods, like baetids, were placed in the Frequent category because they are good swimmers with rapid settling capabilities (Elliott 1971). The Ephemerellidae are weak swimmers with a thick exoskeleton. However, *Ephemerella ignita*, *E. subvaria*, and *E. invaria* were placed in groups that always returned to the bottom faster than dead individuals (Elliott 1971) or were intermediate with respect to settling efficiency (Ciborowski and Corkum 1980; Otto and Sjöström 1986). However, based on their intentional drift response to predators and aggressors (Table 3), I placed *Ephemerella* and all Ephemerellidae in the Rare group. Although Heptageniidae (classified as Occasional in Table 3) are also weak swimmers with an intermediate settling efficiency, they drift more frequently during confrontations, tend to swim more often than Ephemerellidae (Otto and Sjöström 1986), and are agile at regaining a foothold when brought in contact with the substrate (Elliott 1971). Even though Isonychiidae, Siphlonuridae, and Leptophlebiidae (except *Choroterpes* and *Traverella*) are swimmers/clingers (Merritt and Cummins 1995), they were classified as Occasional intentional drifters based on the response of *Leptophlebia*, *Paraleptophlebia*, and *Nesameletus* to predators or aggressors (Table 3). I found no information on the intentional drift propensity of burrowing mayflies (Ephemeridae, Polymitarcyidae) or on mayflies that bury themselves in soft sediments (Caenidae and most Tricorythidae). However, *Ephemera danica* is a weak swimmer and has difficulty in regaining a "foothold" on the substrate (Otto and Sjöström 1986). Burrowing mayflies were therefore classified with other weak swimmers in the Rare subcategory. With no information to indicate otherwise, mayflies that bury themselves in the sediment were classified with burrowers. Except for Perlidae and Taeniopterygidae, all Plecoptera were classified as Rare intentional drifters. Most are poor swimmers (weak side-to-side movements) with an intermediate to low settling efficiency. They often curl into a "U" or "J" shape, increasing their settling rate but decreasing their ability to regain a foothold on the substrate (Otto and Sjöström 1986). Unlike other Plecoptera, Perlidae were assigned to the Occasional category because they use their legs as oars and are strong, agile swimmers (Stewart and Szczytko 1983; Otto and Sjöström 1986; Rader and McArthur 1995). *Taeniopteryx* and *Brachyptera* (Taeniopterygidae) are poor swimmers but because of their drifting posture can readily regain a foothold on the substrate (Madsen 1969; Otto and Sjöström 1986). Both families have an Occasional tendency to intentionally drift during confrontations (Table 3). Trichoptera were separated into case-makers (especially rock cases) with no intentional drift propensity (see *Glossosoma*, Table 3) and net-spinners. Net-spinning caddisflies will occasionally drift during confrontation (see Hydropsychidae and Polycentropidae, Table 3) and will often trail a silk thread to enhance their settling efficiency (Elliott 1971; Otto and Sjöström 1986). Net-spinning Lepidoptera were classified with net-spinning Trichoptera in the Occasional category. Free-living (*Rhyacophila*) and case-making caddis larvae (No Drift) are nonswimmers with poor reattachment abilities (Otto and Sjöström 1986). Except for the Simuliidae, all Diptera (Rare category) were considered nonswimmers with a poor settling efficiency that do not drift during predator–prey or aggressive confrontation (see Blephariceridae and Chironomidae, Table 3). Simuliidae frequently drifted when confronted by predators and they trail a silk thread to increase their settling rate (Hynes 1970; Hemphill 1988; Reidelbach and Kiel 1990). Odonates were placed in the Occasional category based solely on swimming ability. The remaining groups (Elmidae, Oligochaeta, Turbellaria, Gastropoda, and Pelecypoda) were nonswimmers that were placed in the No Drift category.

For a few taxa, empirical evidence (behavioral observations) differed from theoretical predictions based on the presumed relationship between intentional drift frequency and settling efficiency. For example, Perlidae were classified as swimmers but only occasionally drifted during confrontation. Perlid stoneflies are also proficient at crawling (e.g., Corkum 1978) and may drift/swim as a secondary option to avoid confrontation. The ability to predict intentional drift frequency based on traits that determine settling efficiency may be limited if other nondrifting tactics are an equally efficient means of avoiding confrontation. For most taxa, however, settling efficiency and intentional drift frequency should be related because agile crawlers are usually poor swimmers. For example, morphological traits that enhance crawling agility (e.g. dorsoventral flattening) should also diminish swimming ability (e.g., absence of streamlining) and settling efficiency.

Some taxa in Table 3 responded to the same mechanism (e.g., predation) in different studies with different propensities to intentionally drift. Empirical observations could vary because of differences among studies. My estimates of intentional drift frequency will, to some degree, depend on the magnitude of risk associated with each study. For example, different species of predators may represent different levels of risk and therefore invoke different intentional drift frequencies. I was unable to assess the comparative level of risk experienced by individuals in different studies. The most prevalent response (rare, occasional, or frequent) was used to classify each taxa.

Habitat

The next five categories (Habitat, Flow Exposure, Mobility, Drag Index, Drift Distance) were used to classify stream invertebrates with respect to their propensity toward accidental dislodgment by the current. Habitat predicts the frequency of accidental dislodgment based on general habitat differences (Table 1). Habitat is divided into three types: "Hyporheic" (White 1993), "Depositional", and "Erosional" (Ward 1992; Merritt and Cummins 1995). Depositional habitats (e.g.,

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Table 2. Intentional/active drift propensity is shown for 61 invertebrate taxa based on 44 studies.

Taxon	Stimulus	Propensity	Evidence	Reference
Ephemeroptera				
Baetidae				
Baetis bicaudatus	Predators	Frequent	Observations	Peckarsky 1980
Baetis bicaudatus	Predators	Frequent	Observations	Peckarsky and Penton 1989
Baetis buceratus	Aggression	—	Observations	Statzner and Mogel 1985
Baetis phoebus	Predators	Frequent	Observations	Peckarsky 1980
Baetis rhodani	Predators	Frequent	Observations	Williams 1987
Baetis rhodani	Predators	Frequent	Observations	Malmqvist 1986
Baetis rhodani	Predators	Frequent	Observations	Malmqvist and Sjöström 1987
Baetis rhodani	Aggression	Occasional	Observations	Williams 1987
Baetis tricaudatus	Predators	Frequent	Observations	Scrimgeour et al. 1994
Baetis tricaudatus	Predators	Frequent	Drift samples	Corkum and Clifford 1980
Baetis tricaudatus	Predators	Frequent	Observations	Molles and Pietruszka 1983
Baetis tricaudatus	Predators	Frequent	Observations	Soluk and Collins 1988
Baetis tricaudatus	Predators	Frequent	Observations	Walde and Davies 1984
Baetis tricaudatus	Predators	Occasional	Observations	Kohler and McPeek 1989
Baetis tricaudatus	Predators	—	Observations	Scrimgeour and Culp 1994
Baetis tricaudatus	Low food	—	Observations	Kohler 1985
*Baetis tricaudatus**	Flow reduction	—	Drift samples	Corrarino and Brusven 1983
Baetis tricaudatus	—	Frequent	Drift samples	Ciborowski 1983
Baetis vagans	Predators	Frequent	Observations	Williams 1987
Baetis vagans	Predators	—	Drift samples	Corkum and Pointing 1979
Baetis vagans	Aggression	Occasional	Observations	Williams 1987
Baetis vagans	—	Frequent	Observations	Corkum 1978
Baetis sp.	Predators	Frequent	Drift samples	Lancaster 1990
Baetis sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Baetis spp.	Predators	Frequent	Drift samples	Forrester 1994
Baetis spp.	Flow reduction	—	Drift samples	Poff and Ward 1991
Psuedocloeon sp.	Low oxygen	—	Observations	Wiley and Kohler 1980
*Drunella grandis**	Flow reduction	—	Both	Minshall and Winger 1968
Ephemerella altana	Predators	Rare	Observations	Molles and Pietruszka 1983
Ephemerella aurivillii	Predators	Occasional	Observations	Scrimgeour et al. 1994
Ephemerella inermis	—	Occasional	Drift samples	Ciborowski 1983
Ephemerella infrequens	Predators	Rare	Observations	Peckarsky 1980
Ephemerella infrequens	Predators	Rare	Observations	Peckarsky and Penton 1989
*Ephemerella lata**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Ephemerella subvaria	Predators	Occasional	Observations	Williams 1987
Ephemerella subvaria	Predators	Rare	Observations	Peckarsky 1980
Ephemerella subvaria	Predators	Rare	Observations	Soluk and Collins 1988
Ephemerella subvaria	Aggression	Rare	Observations	Williams 1987
Ephemerella sp.	Predators	No Drift	Drift samples	Forrester 1994
Ephemerella sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Eurylophella sp.	Predators	No Drift	Drift samples	Forrester 1994
Heptageniidae				
Cinygmula mimus	Predators	Occasional	Observations	Peckarsky and Penton 1989
Cinygmula sp.	Predators	Occasional	Observations	Peckarsky 1980
Cinygmula sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Epeorus deceptivus	Predators	Occasional	Observations	Peckarsky and Penton 1989
Epeorus longimanus	Flow reduction	—	Drift samples	Poff and Ward 1991
Heptagenia hebe	Predators	—	Observations	Peckarsky 1980
Rhithrogena semicolorata	Predators	Rare	Observations	Williams 1987
Rhithrogena semicolorata	Aggression	Rare	Observations	Williams 1987
Stenacron interpunctatum	Predators	Rare	Drift samples	Walton 1980
*Stenacron interpunctatum**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Stenonema fuscum	Predators	Occasional	Observations	Peckarsky 1980
*Stenonema pulchellum**	Oxygen stress	—	Observations	Wiley and Kohler 1980
Stenonema vicarium	Predators	Occasional	Observations	Williams 1987
Stenonema vicarium	Aggression	Rare	Observations	Williams 1987

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Table 2 (*continued*).

Taxon	Stimulus	Propensity	Evidence	Reference
Stenonema sp.	Predators	No Drift	Drift samples	Forrester 1994
Leptophlebiidae				
Leptophlebia cupida	Predators	Occasional	Drift samples	Corkum and Clifford 1980
Paraleptophlebia adoptiva	Predators	Occasional	Observations	Ode and Wissinger 1993
Paraleptophlebia heteronea	Predators	Frequent	Both	Culp et al. 1991
Paraleptophlebia heteronea	Predators	Occasional	Observations	Scrimgeour et al. 1994
Paraleptophlebia mollis	Aggression	Occasional	Observations	Corkum 1978
Paraleptophlebia spp.	Predators	Occasional	Drift samples	Forrester 1994
Siphlonuridae				
Nesameletus ornatus	Predators	Occasional	Observations	McIntosh and Townsend 1994
Plecoptera				
Leuctridae				
Leuctra fusca	Predators	—	Drift samples	Malmqvist and Sjöström 1987
Nemouridae				
*Nemoura cinctipes**	Flow reduction	—	Both	Minshall and Winger 1968
Perlidae				
Acroneuria abnormis	Aggression (?)	Frequent (?)	Observations	Walton et al. 1977
Acroneuria abnormis	Aggression	Occasional	Observations	Rader and McArthur 1995
Taeniopterygidae				
*Brachypteri risi**	Oxygen stress (?)	—	Observations	Madsen 1969
Taeniopteryx burksi	Predators	Frequent	Drift samples	Walton 1980
Taeniopteryx metequi	Predators	Frequent	Drift samples	Walton 1980
Trichoptera				
Glossosomatidae				
Glossosoma nigrior	Predators	No Drift	Observations	Kohler and McPeek 1989
Hydropsychidae				
Cheumatopsyche sp.	Aggression	Rare	Observations	Glass and Bovbjerg 1969
Hydropsyche bronta	Predators	Occasional	Drift samples	Michael and Culver 1987
Hydropsyche instabilis	Flow reduction	—	Observations	Edington 1965
Polycentropodidae				
Plectrocnemia conspersa	Aggression	Occasional	Observations	Hildrew and Townsend 1980
Rhyacophilidae				
Rhyacophila sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Uenoidae				
Neothremma sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Diptera				
Blephariceridae				
Blepharicera micheneri	Aggression	No Drift	Observations	Dudley et al. 1990
Chironomidae	Predators	—	Drift samples	Malmqvist and Sjöström 1987
Chironomidae	Predators	No Drift	Drift samples	Lancaster 1990
Chironomidae*	Flow reduction	—	Both	Minshall and Winger 1968
Simuliidae	Aggression	—	Observations	Chance 1970
Simuliidae	Aggression	—	Observations	Tonnoir 1925
Simuliidae	Flow reduction	—	Drift samples	Poff and Ward 1991
Cnephia dacotensis	Aggression	—	Observations	Gersabeck and Merritt 1979
Cnephia dacotensis	Flow alteration	—	Observations	Gersabeck and Merritt 1979
Prosimulium fuscum	Predators	Frequent	Observations	Wiley and Kohler 1981
Prosimulium fuscum	Aggression	Rare	Observations	Wiley and Kohler 1981
Prosimulium mixtum	Aggression	—	Observations	Harding and Colbo 1981
Prosimulium mixtum	Aggression	—	Observations	Gersabeck and Merritt 1979
Prosimulium mixtum	Flow alteration	—	Observations	Gersabeck and Merritt 1979
Simulium noelleri	Predators	—	Observations	Wooton and Merritt 1988
Simulium piperi	Aggression	Rare	Observations	Hart 1986
Simulium tuberosum	Predators	Frequent	Observations	Wiley and Kohler 1981
Simulium tuberosum	Aggression	Rare	Observations	Wiley and Kohler 1981
Simulium virgatum	Predators	Frequent	Observations	Hemphill 1988

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Table 2 (*concluded*).

Taxon	Stimulus	Propensity	Evidence	Reference
Simulium vittatum	Predators	Frequent	Observations	Hansen et al. 1991
Simulium sp.	Predators	—	Observations	Fuller and DeStaffan 1988
Simulium sp.*	Flow reduction	—	Drift samples	Corrarino and Brusven 1983
Simulium sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Simulium spp.	Aggression	—	Observations	Disney 1972
Tricladida				
Planariidae				
Dugesia sp.*	Flow reduction	—	Both	Minshall and Winger 1968
Amphipoda				
Gammaridae				
Gammarus pulex	Predators	—	Drift samples	Malmqvist and Sjöström 1987

Note: "Stimulus" indicates the mechanisms ("Predators", "Aggression", "Food", and "Oxygen") producing an intentional drift response. The mechanisms producing drift are not known for studies manipulating flow. "Frequent", "Occasional", and "Rare" indicated intentional drift propensity and was only determined where (1) the percentage drifting of the total number of nymphs was known, (2) the percentage of drift behavior was compared with other responses (e.g., crawling, remaining stationary), or (3) the authors made explicit statements regarding drift frequency. "No Drift" indicates the absence of intentional drift to a specific stimulus. "Evidence" describes the methods used to determine an intentional drift response. Studies using drift samples without behavioral observations were used only when authors explicitly stated that drift was intentional. A dash indicates that information was not sufficient to make a decision on the appropriate classification. An asterisk indicates studies where the stimulus fluctuated beyond the normal range of variation (i.e., disturbance/catastrophic drift).

pools and margins) form under baseflow conditions but do not include small pockets of slow water and redeposited materials in erosional reaches (e.g., riffles). I assume that organisms residing within the hyporheos are not accidentally dislodged and that macroinvertebrates inhabiting depositional areas contribute less to the drift than invertebrates from erosional habitats. Macroinvertebrates in depositional habitats are less likely to be dislodged and can rapidly return to the benthos (Waters 1962; Bailey 1966; Campbell 1985). Therefore, I assigned a greater score for taxa that primarily reside in erosional (9) compared with depositional (1) habitats. In the Rocky Mountains, nymphs in the families Capniidae, Leuctridae, Taeniopterygidae, and Chloroperlidae spend most of their aquatic existence as part of the hyporheic fauna (e.g., Ward and Kondratieff 1992; DeWalt et al. 1994; DeWalt and Stewart 1995). Large taxa (e.g. *Sweltsa* spp.) are probably an exception. Such taxa should be assigned to erosional habitats because they appear in the surface benthos long before emergence (Mackay 1969; Harper et al. 1991).

Flow exposure

Flow Exposure group classification was recently proposed to provide insight into the response of macroinvertebrates to small-scale flow conditions (Growns and Davis 1994). Whereas Habitat was used to classify invertebrates on a larger scale according to preferred units within stream reaches, Flow Exposure is an indication of flow preferences within habitat units. Growns and Davis (1994) partitioned invertebrates from streams in Australia into groups experiencing differing degrees of exposure to near-bed flows. "Avoiders" spent most of their life cycle within the substratum out of direct contact with the flow. Avoiders included taxa that dug burrows or buried themselves in fine sediment. "Facultatives" were invertebrates that often occurred in exposed areas (e.g., upper surfaces), but had the ability to move into protected crevices. "Obligates" (Hydroptilidae, Blephariceridae, Tanytarsini, Psephenidae, net-spinning Trichoptera) were fully exposed to the water column for most of their life cycle and had behavioral (e.g., fixed retreats) or morphological (e.g., hydraulic suckers) adaptations for attachment. Simuliidae were placed in the Facultative category, but were difficult to classify because they can move from one fixed location to another and yet are fully exposed to the current. In this paper, Chironomidae were separated into free-living taxa (Avoiders) and those that were primarily tube-dwellers (Tanytarsini, *Cardiocladius*, *Cricotopus*) of the Obligate group. Both Hynes (1970) and Growns and Davis (1994) provide several examples of each Flow Exposure group. I propose that Flow Exposure groups can help to estimate the likelihood of dislodgment. Adaptations that prevent dislodgment are usually less efficient in Facultatives than in Obligates because Facultatives are more mobile. I assume an evolutionary tradeoff between mobility and attachment; adaptations that enhance attachment efficiency reduce mobility and dislodgment. Therefore, Facultatives should be accidentally dislodged more frequently than Obligates. For example, the more mobile *Stenacron interpunctatum* was accidentally dislodged more frequently at high current velocities (25.0 $cm \cdot s^{-1}$) than the slower, less agile *Taeniopteryx* spp. (Walton 1980). Also, Ciborowski (1987) surveyed the literature which included numerous taxa representing a wide range of mobility and found that drift frequency was positively correlated with benthic locomotory ability.

Mobility

Because of the probable tradeoff between mobility and attachment, the propensity to drift should also be affected by various levels of mobility (Corkum 1978; Ciborowski 1987). I make the general assumption that greater mobility increases the likelihood of dislodgment. Therefore, the likelihood of dislodgment descends from swimming > crawling > attached > sessile. Mobility subcategories are based only on mobility/attachment traits and differ from other similar categories (e.g., skaters, clingers, sprawlers from Merritt and Cummins 1995) in that they do not include a description of invertebrate habits or modes of existence. "Sessile" macroinvertebrates (e.g. late-instar Hydroptilidae) remain fixed in one position for most of their aquatic existence or as long as they are part of the epibenthic habitat. "Attached" taxa (e.g., Brachycentridae, Simuliidae, net-spinning caddisflies) are typically fastened in one position for days or weeks but can move, if necessary, to new locations in response to changing conditions. "Crawlers" include a wide range of taxa (e.g., Heptageniidae, Gastropoda, Glossosomatidae) that move with varying degrees of speed and agility. Crawlers have various morphological adaptations that also enhance attachment (sharp tarsal crawls, sucker-like ventral gills, a setal disk), but they rarely remain in the same place for more than a day and they must move in order to feed. Blephariceridae and Psephenidae were placed in the Attached category because of their slow mobility and exceptionally efficient adaptations to the current. "Swimmers" (Baetidae, Siphlonuridae,

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Table 3. Invertebrate intentional drift propensity based on their response to mechanisms (predation and aggression) that influence drift frequency.

Taxon	Predators	Aggression
Ephemeroptera		
Baetidae		
Baetis	Frequent (91%); Occasional (9%)	Frequent (100%)
Ephemerellidae		
Ephemerella	Occasional (25%); Rare (63%); No Drift (12%)	Rare (100%)
Eurylophella	No Drift (100%)	—
Heptageniidae		
Cinygmula	Occasional (100%)	—
Epeorus	Occasional (100%)	—
Rhithrogena	Rare (100%)	Rare (100%)
Stenocron	Rare (100%)	—
Stenonema	Occasional (67%); No Drift (33%)	Rare (100%)
Leptophlebiidae		
Leptophlebia	Occasional (100%)	—
Paraleptophlebia	Frequent (25%); Occasional (75%)	Occasional (100%)
Sipholnuridae		
Nesameletus	Occasional (100%)	—
Plecoptera		
Perlidae		
Acroneuria	—	Frequent ? (50%); Occasional (50%)
Taenopterygidae		
Taeniopteryx	Occasional (100%)	—
Trichoptera		
Glossomatidae		
Glossosoma	No Drift (100%)	—
Hydropsychidae		
Cheumatopsyche	—	Rare (100%)
Hydropsyche	Occasional (100%)	—
Polycentropidae		
Plectrocnemia	—	Occasional (100%)
Diptera		
Blephariceridae		
Blepharicera	—	No Drift (100%)
Chironomidae	No Drift (100%)	—
Simulidae		
Prosimulium	Frequent (100%)	Rare (100%)
Simulium	Frequent (100%)	Rare (100%)

Note: Only studies indicating the intentional drift frequency were used (Table 2). A dash indicates categories where no information was available. Numbers in parentheses are the percentage of studies indicating the designated response. See Table 2 for the sample size of studies and species comprising each taxon.

Leptophlebiidae) are streamlined taxa that are capable of directional "porpoise-like" swimming undulations (Hynes 1970; Wilzbach et al. 1988). Taxa with side-to-side thrashing movements (e.g., Rhyacophilidae, Tipulidae, most Chironomidae) produce very weak directional locomotion and were not classified with Swimmers. No attempt was made to relate various types of crawling locomotion or various degrees of crawling and swimming agility (e.g., Baetidae versus Siphlonuridae) to increasing or decreasing propensity toward accidental dislodgment. Mobility characteristics were only determined for taxa that reside in the epibenthic habitat. Taxa from depositional or hyporheic habitats were not classified (NA).

Drag index

Almost all invertebrates that venture from low-flow microhabitats will experience drag caused by a turbulent, three-dimensional microflow environment (Nowell and Jumars 1984). Very few, if any, invertebrates large enough to be eaten by trout (>1.0 or 2.0 mm) can reside within the boundary layer of a stream, especially in high-gradient streams typical of the Rocky Mountains. The Drag Index relates invertebrate size and shape to the probability of dislodgment. The force necessary to dislodge individual organisms is equivalent to the current velocity passing though its frontal projection area. The amount of drag experienced by stream organisms subjected to identical microflow conditions is a function of both body size and shape which will determine the difference in the amount of pressure impending on the front (upstream, high pressure zone) compared with the rear (downstream, low-pressure turbulent zone) of an invertebrate (Vogel 1994). Because habitat selection, flow exposure, and morphological adaptations related to attachment and mobility will also determine the propensity toward accidental dislodgment, some measure of drag by itself is not an adequate estimation of the likelihood to accidentally drift. For this reason the preceding three categories (Habitat, Flow Exposure, and Mobility) were included (Table 1). Wilzbach et al. (1988) suggested that body shape, expressed as the ratio of height to width, was a reasonable index of drag and the propensity to become dislodged. They found that as the height to width ratio increased, drag increased and the current velocity required to dislodge killed individuals decreased. Stream invertebrates can be classified into four morphological types based on their general body shape: (*i*) streamlined, (*ii*) cylindrical, (*iii*) dorsoventrally flattened, and (*iv*) spherical/globular. Some cylindrical invertebrates are more round in cross section (Tipulidae), whereas others are somewhat compressed in the dorsoventral direction (Perlidae). All invertebrate taxa were assigned to one of the four morphological types and the height to width ratio was measured for each (Table 4). The height to width ratio was then combined with body size to calculate the Drag Index (see below). Body size (length of invertebrate in the direction of the flow) will also influence the amount of drag experienced by stream invertebrates (Vogel 1994). For example, large (45 mm) Tipulidae (height/width ≈ 1.0) will experience greater drag under similar microflow conditions than small Tipulidae (15 mm). Streamlined taxa (e.g., Baetidae) were a special case because their bodies were designed to reduce drag (Vogel 1994). They were automatically assigned to the subcategory with the lowest score (1) regardless of the magnitude of their Drag Index. For stream invertebrates inhabiting the epibenthic habitat, I propose combining both shape and size in one index. The Drag Index (D) can be calculated as follows:

$$D = (H/W)\cdot L$$

where L is body length (cerci excluded) and H and W are the maximum body height and width. H and W were measured using calipers accurate to 0.02 mm whereas L was determined by calculating the midmost length of the size ranges for each taxon (see Table 4). Trichoptera were measured in their cases or tubes. Under similar microflow conditions, very small (length <5.0 mm) or dorsoventrally flattened taxa ($D < 6.0$) should experience less drag than taxa with a large height/width. Index values <6.0 included invertebrates (*Psephenus*, *Rhithrogena*) known to experience reduced drag (Wilzbach et al. 1988). However, intermediate-sized (5.0–20.0 mm) cylindrical/spherical taxa ($6.0 > D < 12.0$) and large (>20.0 mm) cylindrical/spherical taxa ($D > 12.0$) should experience intermediate and high levels of drag, respectively. Cutoff points defining high, intermediate, and low levels of drag were not empirically determined.

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Table 4. Calculations used to determine the Drag Index (*D*) of various taxa.

Taxon	Type	Ratio	*L*	*D*	*n*
Ephemeroptera					
Baetidae	1	0.79	6.0	4.7	6
Ephemerellidae					
Drunella grandis	2	0.68	14.0	9.5	6
Drunella doddsi	2	0.57	14.0	8.0	7
Attenella	2	0.70	7.0	4.9	4
Ephemerella	2	0.74	10.0	7.4	8
Serratella	2	0.60	7.0	4.2	5
Heptageniidae	3	0.47	12.5	5.9	10
Leptophlebiidae					
Chloroterpes	1	0.51	6.5	3.3	3
Paraleptophlebia	1	0.65	8.0	5.2	6
Traverella	1	0.55	8.5	4.7	3
Isonychiidae					
Isonychia	1	0.80	14.0	11.2	5
Siphlonuridae					
Ameletus		0.71	10.0	7.1	8
Plecoptera					
Chloroperlidae	2	0.65	15.0	9.8	10
Nemouridae	2	0.72	7.5	5.4	8
Perlidae	2	0.07	22.5	1.5	10
Perlodidae	2	0.69	14.0	9.7	10
Pteronarcydae	2	0.71	35.0	24.9	6
Trichoptera					
Brachycentridae	2	1.00	9.0	9.0	6
Glossosomatidae	2	0.81	5.5	4.5	10
Helicopsychidae	2	0.67	5.0	3.4	8
Muscidae	2	1.00	8.0	8.0	0
Psychodidae					
Maruina	2	0.70	4.5	3.2	5
Simuliidae	2	1.65	3.3	5.4	10
Stratiomyidae	2	0.58	10.0	5.8	6
Tabanidae	2	1.14	30.0	34.2	2
Tanyderidae	2	1.00	11.0	11.0	0
Tipulidae					
Antocha	2	0.93	18.0	16.7	3
Dicranota	2	1.00	18.0	18.0	5
Hexatoma	2	1.00	45.0	45.0	3
Limnophila	2	1.00	30.0	30.0	0
Limonia	2	1.00	16.0	16.0	6
Pedicia	2	1.00	16.0	16.0	6
Rhabdomastix	2	1.00	18.0	18.0	0
Tipula	2	1.10	45.0	49.5	2
Hydropsychidae	2	0.99	19.0	18.8	10
Hydroptilidae	2	0.27	2.5	0.7	8
Lepidostomatidae	2	1.00	9.0	9.0	6
Leptoceridae	2	1.00	12.5	12.5	3
Uenoidae	2	0.94	12.0	11.3	10
Limnephilidae					
Allomyia	2	1.00	22.0	22.0	2
Dicosmoecus	2	1.00	19.5	19.5	6
Ecclisomyia	2	1.00	12.0	12.0	0
Glyphopsyche	2	1.00	19.5	19.5	0
Hesperophylax	2	1.00	20.5	20.5	6
Limnephilus	2	1.00	17.0	17.0	0
Onocosmoecus	2	1.00	16.0	16.0	0
Psychoglypha	2	1.00	19.5	19.5	2
Psychoronia	2	1.00	19.5	19.5	0
Pycnopsyche	2	1.00	18.5	18.5	0
Philopotamidae	2	1.00	12.0	12.0	3
Polycentropodidae	2	1.00	24.0	24.0	5
Psychomyiidae	2	1.00	6.0	6.0	0
Rhyacophilidae	2	0.73	13.5	9.9	10
Diptera					
Athericidae	2	1.03	15.0	15.5	8
Blephariceridae	2	0.59	7.5	4.4	6
Chironomidae	2	1.00	5.0	5.0	10
Deuterophlebiidae	3	0.46	3.0	1.4	5
Empididae	2	1.00	4.5	4.5	8
Coleoptera					
Dryopidae adult	4	0.64	7.0	4.5	5
Elmidae larva	2	0.84	6.0	5.0	6
Elmidae adult	4	0.77	5.0	3.9	6
Psephenidae	3	0.37	4.5	1.7	6
Odonata	2	0.63	25.0	15.8	6
Lepidoptera					
Petrophila	2	0.80	18.0	14.4	3
Megaloptera					
Corydalidae	2	0.65	16.0	10.4	5
Sialidae	2	0.60	21.0	12.6	5
Turbellaria	2	0.40	7.5	3.0	6
Amphipoda	2	1.95	8.5	16.6	10
Gastropoda	4	0.83	8.0	6.6	8
Hydracarina	4	0.46	2.0	0.9	6

Note: Type refers to one of four general morphological types for stream invertebrates (1 = streamlined, 2 = cylindrical, 3 = dorsaventrally flattened, and 4 = spherical/globular). Ratio and *L* are the average height/width and the size range midpoint based on body length (mm), respectively. *n* is the number of individuals measured to determine the height/width. A "0" indicates where the height/width was inferred from other closely related taxa. Taxa that spend most of their life cycle in the hyporheic zone are not included (e.g., Capniidae and Leuctridae).

In the absence of data to indicate otherwise, cutoff points (6 and 12) were determined by visual inspection of the exponential relationship between the drag of morphologically different taxa and current velocity (Wilzbach et al. 1988). If current velocity can be measured at the scale of an individual organism, then the Drag Index (*D*) can be combined with Reynolds number (Re). Reynolds number is based on body size and has been used to estimate pressure drag and the force of microcurrent conditions (Vogel 1994):

$$\mathrm{Re} = (U \cdot D)/v$$

where U is the average velocity of the fluid and v is the kinematic viscosity. Because both shape (height/width) and body size are important, substituting the Drag Index for body size in calculating Reynolds number should provide a more accurate estimate of the drag exerted on stream invertebrates.

Drift distance

Availability depends on both accidental drift frequency and the distance traveled during a drift event. Dislodged invertebrates that

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quickly return to the benthos should be less available than those that remain in the water column. Habitat (e.g., riffle versus pool) will influence both frequency and distance, whereas Flow Exposure, Mobility, and the Drag Index primarily influence only drift frequency. Drift Distance was determined by settling efficiency which also provided part of the criteria used to classify invertebrates based on their intentional drift propensity. However, the effects of settling efficiency are reversed when considering accidental versus intentional drift. For intentional drifters, the ability to efficiently exit the drift should increase availability by increasing the propensity to intentionally drift at twilight. With respect to accidental drift, however, settling efficiency will decrease the time in the drift and, therefore, availability. For example, *Baetis* is an active swimmer that frequently deliberately drifts (a score of 9 in the Intentional Drift category) but can quickly return to the substrate when dislodged (a score of 1 in the Drift Distance category). Traits that determine drift distance and settling efficiency were included as components of availability with respect to both intentional and accidental drift.

Elliott (1971) separated invertebrates into three groups: (*i*) passive drifters that travel as far as dead individuals at slow and fast current velocities, (*ii*) typically passive drifters that could return to the bottom faster than dead individuals at slow, but not fast current velocities, and (*iii*) active settlers that return to the bottom faster than dead individuals at all current velocities. The ability to actively return to the bottom depends on three traits: (*i*) swimming ability, (*ii*) agility in regaining a foothold, and (*iii*) sinking postures. Because taxa that actively settle differ in settling efficiency (Elliott 1971) and because taxa that passively settle can either float or sink, the active–passive dichotomy was not sufficient to predict differences in drift distance and availability. Based on the literature (McLay 1970; Elliott 1971; Ciborowski and Corkum 1980; Otto and Sjöström 1986; Allan and Feifarek 1989), I divided taxa that actively returned to the substrate into two groups: "Active Swimmers" (Baetidae, Amphipoda, Perlidae) and "Active Settlers" that were weaker swimmers and (or) used various sinking postures (Ephemerellidae and most Plecoptera) and efficient ways of regaining a foothold (claws and silk) on the substrate (e.g., Heptageniidae, Ephemerellidae, Simuliidae, Rhyacophilidae, net-spinning Trichoptera). Passive settlers were also divided into two groups based on buoyancy characteristics. "Sinkers" (Trichoptera with rock cases, clams, and snails) were negatively buoyant taxa that readily settle out of the drift (e.g., Otto 1976). Other taxa ("Floaters") that slowly floated to the bottom (no ballast) and lacked reattachment capabilities (claws, silk) were assigned to the farthest drifting category (a score of 6). Turbellaria, Diptera (except Simuliidae), and some Trichoptera with cases constructed of plant materials (e.g., Brachycentridae) were classified as Floaters.

Adult Drift

Ovipositing and emergence behavior and diel activity were used to classify emerging nymphs and aerial adults with respect to their occurrence in the drift and exposure to fish predation. Many taxa that are largely unavailable as immatures can become an important food resource during relatively brief periods of transition between the aquatic and terrestrial environment. Emerging adults that drift or swim to the surface are more available than those that crawl to the bank or emerge in winter. Similarly, adults that run across the water or land on the surface are more susceptible than adults that crawl into the water or drop their eggs from the air. Adults that avoid the water and lay their eggs on overhanging vegetation or recently exposed rock surfaces are least available to fish. Plus, adults that are active (ovipositing, mating, dispersal/flying) during the day, including morning and evening twilight periods (crepuscular activity), were deemed more available than primarily nocturnal taxa (e.g., most Trichoptera). Although many adult Trichoptera may begin activity during the evening hours, most taxa do not reach peak activity until well after sunset and twilight.

Benthic exposure

The "Benthic Exposure" category was similar to the "Flow Exposure" category except it does not refer to dislodgment by the current and the propensity to drift, but to the location of macroinvertebrates in or on the substrate with respect to trout detection and benthic feeding behavior. Despite conceptual differences, these two traits were correlated and somewhat redundant. For many taxa, flow exposure and benthic exposure were based on the same microspatial traits (e.g., flow avoiders were almost always concealed within the substrate). I adopted the rationale that if two categories were redundant for most taxa, but can help resolve differences in availability for a few, they both were included. For example, taxa classified as Obligates in the Flow Exposure category (e.g., net-spinning caddisflies) were fully exposed to the current, but may have been concealed between substrate crevices (i.e., classified as "Concealed" in the Benthic Exposure category). Benthic Exposure separated taxa that dig burrows, were buried in fine sediment, or occurred in the hyporheic zone from those that spent the majority of their aquatic existence in the epibenthic habitats (concealed or exposed). Concealed invertebrates typically occurred in crevices or on substrate undersurfaces whereas "Exposed" taxa resided on upper sunlit surfaces. Although many taxa can use both concealed and exposed surfaces (Heptageniidae), most predominantly occurred in one or the other during the day. I make the assumption that salmonids do not have the low-light visual acuity necessary to feed on the bottom substrate at night. Therefore, the movement of invertebrates from concealed surfaces during the day to exposed at night (Rader and Ward 1990; Culp et al. 1991) was not relevant behavior that might influence availability. However, if such benthic movements take place at twilight and increase the probability of accidental dislodgment, then this behavior might increase availability depending on the invertebrate's propensity towards accidental dislodgment. The propensity to become accidentally dislodged has already been estimated by classifying taxa based on previously defined traits. Macroinvertebrates that occur within moss or thick filamentous algae were classified as Concealed. Based on quantitative observations of salmonid foraging behavior during the day in the field, Bachman (1984) found that adult brown trout (*Salmo trutta*) consumed nearly 87% of their prey from the drift and removed less than 15% directly from the bottom substrate. Gowan (1995) found that only 5% of brook trout (*Salvelinus fontinalis*) daytime feeding forays were benthic (95% were in the drift). (There are no data, that I am aware of, pertaining to the proportion of benthic versus drift forays by salmonids at night.) Therefore, the lower subcategory scores for Benthic Exposure (Concealed = 1 and Exposed = 3) reflect salmonid preferences for feeding in the drift. All drift categories have at least one subcategory with a score of 6 or 9.

Size

The "Size" category was based on the body length (cerci excluded) of late-instar larvae. Early-instar larvae are often buried in the hyporheic zone or too small to be available as food for juvenile and adult trout (Wilzbach et al. 1986). Species descriptions in taxonomic keys provided size ranges for each taxa. Invertebrates were assigned to Size subcategories based on their size range midpoint. Separate size ranges for adult aquatic insects were not used because late-instar and adult size ranges were almost always identical. As trout grow, they select larger invertebrates that provide a greater energy return but never completely ignore smaller prey (Ringler 1979; Allan 1981). Wankowski and Thorpe (1979) suggested that prey profitability would increase with prey size up to some optimum and then decline with larger prey because of increased "handling" costs. The optimum prey size would be 10.0–20.0 mm long for a 20.0- to 30.0-cm trout. Prey <1.0 mm rarely constitute a substantial portion of salmonid diets (e.g., Skinner 1985; Hubert and Rhodes 1992; Bozek et al. 1994). However, if sufficiently abundant, some taxa <1.0 mm can be occasionally consumed (Young et al. 1997). Therefore, taxa <1.0 mm were given a score of 1 instead of 0. All else being equal (e.g., abundance),

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invertebrates between 1.0 and 5.0 mm are small but commonly consumed (Skinner 1985; Bozek et al. 1994). Taxa in the 5.1- to 20.0-mm range are often disproportionately selected by feeding salmonids (Allan 1981; Skinner 1985). Taxa >20.0 mm are exceptionally large and presumably difficult to handle. Size subcategory scores reflect this hump-shaped relationship between profitability and prey size (Wankowski and Thorpe 1979). Therefore, small (1.0–5.0 mm) and very large (>20.0 mm) taxa are assigned a score of 3 and taxa between 5.1 and 20.0 mm are given a score of 9. Size rankings are based on the selectivity of juvenile and adult trout with body lengths between 6.0 and 30 cm. YOY trout are usually <6 cm and often feed directly from the bottom (e.g., Hubert and Rhodes 1992).

Abundance

Because salmonids tend to specialize on the most frequently consumed prey in its recent feeding history, availability is, in large part, defined by abundance (Allan 1981). "Abundance" will interact with the propensity to drift (intentional or accidental), adult drift, benthic exposure, and size to determine availability. For example, abundant taxa of adequate size with a strong propensity to drift (intentional and accidental) should be most available as food for trout. Rare taxa, however, will have a low availability regardless of their size and propensity to drift, and taxa that seldom drift or are small (<1.0 mm) will have a low availability regardless of their abundance. Therefore, the subtotal scores for each taxon based on intentional drift, dislodgment, adult drift, benthic exposure, and size (traits of Table 1) were multiplied by a factor expressing the differing affects of abundance on availability. The subtotal from Table 1 for rare taxa was reduced by one half (multiplied by 0.5) to produce the final availability score. The availability of rare taxa is low regardless of other traits (drift propensity and size). However, the availability of abundant and common taxa will be influenced by all three (drift propensity, size, and abundance). Therefore, abundant taxa with subtotal scores (based on drift propensity and size; Table 1) equal to or greater than the average (mean subtotal score = 36) were increased by 50% (multiplied by 1.5). Abundant taxa with subtotals less than the average did not occur. If they did, however, they should be multiplied by 1.0 (i.e., the effect of a high abundance should be offset by a less than average score on drift propensity and size). Similarly, common taxa with a subtotal score greater than the average or equal to and less than the average were increased by a factor of 1.2 or 1.0, respectively.

Invertebrates were assigned to specific abundance categories based primarily on notes found in regional keys. "Rare" taxa were relatively easy to recognize because they were consistently among the least collected taxa throughout their range. Only three taxa (*Baetis*, Simuliidae, and Chironomidae) were designated as "Abundant". All other macroinvertebrates were classified as "Common". Abundant and Common designations were difficult because some invertebrates may be abundant in one location and common in another depending on changing environmental conditions. Abundance designations based on quantitative samples would increase accuracy and the model's ability to predict availability.

Data analysis

Spearman's rank correlation was used to determine the significance of the association between the predicted rankings and the relative abundance (percent by numbers) based on actual fish gut data. A priori rankings were compared to three data sets that quantified the number of both immature and adult macroinvertebrates. Allan (1978) examined the gut contents of 18 adult brook trout from Cement Creek, a third-order tributary of the East River in Colorado. Bozek et al. (1994) and Young et al. (1997) examined gut contents from 20 and 37 adult Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*), respectively, taken from the same drainage in the headwaters of the North Fork of the Little Snake River. Cement Creek and the North Fork of the Little Snake River are located at similar elevations within the montane zone of the central Rocky Mountains (Colorado and Wyoming).

Because of difficulties associated with catching trout, the primary deficiency of most gut analyses is their failure to detect the importance of taxa that contribute to energy consumption but are absent from guts during sampling. Gut samples will characterize invertebrate availability for the previous 12–24 h at a spatial scale determined by fish movements. For example, gut samples from resident trout that forage from a single location will characterize invertebrate availability for a relatively small stream section. Most trout gut analyses are based on relatively small sample sizes (20–25 gut samples). Studies of trout diets at large spatial scales and over the course of a complete growing season are time intensive and therefore rare. The relative importance of different invertebrate taxa in salmonid diets based on gut analysis may exclude important taxa. Gut analyses should, however, reflect the rank order of availability for the taxa that do occur in the guts and they should not include relatively unavailable taxa. Therefore, if this index is efficient at ranking taxa based on their availability to drift-feeding salmonids, then (*i*) the rank abundance of taxa in guts should be correlated with rankings based on the index, (*ii*) gut samples should not include the least available taxa as identified by this index, and (*iii*) some taxa, present in the benthos and known to be important in salmonid diets, might be absent because of sampling deficiencies. These three studies were chosen because of their location in the Rocky Mountains and because both immature and adult insects were counted and benthic samples collected (Allan 1978; Bozek et al. 1994; Young et al. 1997). Benthic samples helped to identified taxa present in the stream but, because of possible sampling deficiencies, were absent from gut analyses. These analyses are preliminary tests. They do not validate the accuracy of this index in determining invertebrate availability to drift-feeding salmonids. Validation may require field studies relating the presence of highly ranked invertebrate taxa with drift abundance and numerous trout gut samples.

One objective of this research was to identify similar taxa (guilds) based on traits that determine availability. Initially, taxa were separated into groups based on the ranking procedure described previously. Groups were identified by gaps of seven or more points between consecutively ranked taxa (see Results). For comparison, a hierarchical cluster analysis (Gauch 1982) was also used to group taxa with similar availability traits. In this analysis, taxa were assigned to groups based on the minimum Euclidean distance between an individual taxon and the center of the most similar cluster. The final result was a dendrogram. Nonhierarchical cluster analyses classify taxa based on an optimization routine: minimization of the pooled within-cluster variance (O'Muircheartaigh and Payne 1977). This nonhierarchical technique was run using ISODATA software (Ball and Hall 1967) and differed from the hierarchical procedure in that it does not produce a dendrogram, but did calculate an R^2 correlation coefficient for each variable/category and the total amount of variation explained by the analysis. Both cluster analyses used data from Table 5: 95 rows (taxa) and 12 columns (categories). Data in the body of the table consisted of subcategory scores assigned to taxa from Table 1. Subcategories that did not apply to some taxa (NA in Table 5) were treated as zeros. None of the data (subcategory scores) were standardized. Therefore, categories with wide-ranging values were weighted heavier than categories with scores of smaller magnitude. This was a convenient way of emphasizing categories (e.g., Habitat) that are known to have an important impact on availability. Since "Abundance" was treated as a multiplier (category subtotal scores were multiplied by a value (0.5, 1.0, 1.2, 1.5) reflecting the importance of abundance on availability), it had an important impact on the assignment of taxa into availability groups. However, "Abundance" is the most likely invertebrate attribute to vary across space and time. For comparison (to analyze the effects of "Abundance"), each analysis (the ranking procedure and both cluster analyses) was rerun excluding "Abundance" as a multiplier and only using the traits of

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Table 5. Subcategory scores are shown for each taxon found in mid- to small-sized streams of the Rocky Mountains.

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Ephemeroptera															
Baetidae															
Acentrella	9?	9	6	9	1	1	6	3	6	3	4–8	9	C	74.4	3.0
Baetis	9	9	6	9	1	1	6	3	6	3	4–8	9	A	93.0	1.0
Callibaetis	9?	1	NA	NA	NA	NA	6	6?	6	3	6–10	9	R	20.0	(57.5)
Diphetor	9?	9	6	9	1	1	6	3	6	3	4–8	9	R	31.0	42.0
Caenidae	1?	1	NA	NA	NA	NA	6	6	6	0	2–6	3	R	11.5	(82.0)
Ephemerellidae															
Attenella	1?	9	6	3	1	3	6?	6	6	1	5–9	9	R	25.5	(46.5)
Drunella	1?	9	6	3	3	3	6	6/3	6	1	8–20	9	C	63.6	(6.5)
Ephemerella	1	9	6	3	3	3	6	6/3	6	1	6–14	9	C	63.6	(6.5)
Serratella	1?	9	6	3	1	3	6?	6	6	1	5–9	9	C	61.2	(11.0)
Timpanoga	1?	1	NA	NA	NA	NA	6	6	6?	0	12–15	9	R	14.5	(72.0)
Ephemeridae	1?	1	NA	NA	NA	NA	6	6	1/6	0	12–24	9	R	12.0	(79.5)
Heptageniidae	3	9	6	3	1	3	6	6	6	1	7–18	9	C	63.6	(6.5)
Isonychiidae	3?	9	6	3/9	3	3	3/6	6	6	1	10–18	9	R	26.0	45.0
Leptophlebiidae															
Choroterpes	3?	9	6	3	1	3	6	6?	6	1	5–8	9	R	26.5	44.0
Leptophlebia	3	1	NA	NA	NA	NA	6	6	6	1	7–15	9	R	16.0	(68.5)
Paraleptophlebia	3	9	6	3/9	1	3	6	6	6	1	6–10	9	C	63.6	(6.5)
Traverella	1?	9	6	3	1	3	6	6?	6	1	7–10	9	R	25.5	(46.5)
Polymitarcyidae	1?	1	NA	NA	NA	NA	6	6	1/6	0	12–17	9	R	12.0	(79.5)
Siphlonuridae															
Ameletus	3?	9	6	3/9	3	3	3	6	6	1	6–14	9	C	62.4	(9.5)
Parameletus	3?	1	NA	NA	NA	NA	3	6?	6	1	10–13	9	R	14.5	(72.0)
Siphlonurus	3?	1	NA	NA	NA	NA	3	6	6	1	10–20	9	R	14.5	(72.0)
Tricorythidae	1?	1	NA	NA	NA	NA	6	6	6	0	4–8	9	C	23.0	49.0
Plecoptera															
Capniidae	1?	0	NA	NA	NA	NA	0	6?	6	0	5–10	9	C	16.0	(68.5)
Chloroperlidae															
Alloperla	1?	0	NA	NA	NA	NA	3	6	6?	0	8–13	9	C	19.0	(61.0)
Paraperla	1?	0	NA	NA	NA	NA	3	6	6?	0	18–20	9	R	12.5	(77.0)
Plumiperla	1?	0	NA	NA	NA	NA	3	6	6?	0	6–8	9	C	19.0	(61.0)
Suwallia	1?	0	NA	NA	NA	NA	3	6	6?	0	8–10	9	R	12.5	(77.0)
Sweltza	1?	9	6	3	3	3	3	6	6	1	12–18	9	C	60.4	12.0
Triznaka	1?	0	NA	NA	NA	NA	3	6	6?	0	6–8	9	R	12.5	(77.0)
Leuctridae	1?	0	NA	NA	NA	NA	3/0	6	6	0	6–10	9	C	19.0	61.0
Nemouridae	1?	9	6	3	1	3	3/0	6	6	1	5–10	9	C	57.6	14.0
Perlidae	3	9	6	3	6	1	3	6	1	1	20–40	3	C	50.4	23.0
Perlodidae	1?	9	6	3	3	3	3	6	1	1	8–20	9	C	54.0	(15.5)
Pteronarcyidae	1?	9	6	3	6	3	3	3	1/6	1	25–50	3	C	46.8	34.0
Taeniopterygidae	3	0	NA	NA	NA	NA	0/3	0	6?	0	6–10	9	R	9.0	(86.5)

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Table 5 (*continued*).

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Trichoptera															
Brachycentridae	0?	9	1	1	3	6	6	6	1	3	6–12	9	C	54.0	(15.5)
Glossosomatidae	0	9	6	3	1	0	6	3	1	3	3–8	9	C	49.2	(26.5)
Helicopsychidae	0?	9	6	3	1	0	6	3?	1	3	4–6	9	C	49.2	(26.5)
Hydropsychidae	3	9	1	1	6	3	6	3	1	1	10–28	9	C	51.6	(20.0)
Hydroptilidae	0?	9	1	0	1	NA	6	3	1	3	1–5	3	C	29.0	43
Lepidostomatidae	0?	9	6	3	3	0	6	3	1	1	7–11	9	C	49.2	(26.5)
Leptoceridae	0?	9	6	3	6	0	6	6	1	1	10–15	9	R	23.5	(48.0)
Limnephilidae															
Allomyia	0?	9	6	3	6	0	6	0	1	1	18–26	3	R	17.5	(65.0)
Dicosmoecus	0?	9	6	3	6	0	6	3	1	1	6–23	3	C	45.6	(35.5)
Ecclisomyia	0?	9	6	3	6	0	6	3?	1	1	10–14	9	R	22.0	50.0
Glyphopsyche	0?	1	NA	NA	NA	NA	6	0?	1	1	16–23	3	R	6.0	94.0
Hesperophylax	0?	9	6	3	6	0	6	0	1	1	18–23	3	C	42.0	(38.5)
Limnephilus	0?	9	6	3	6	0	6	0	1	1	10–24	9	C	49.2	(26.5)
Onocosmoecus	0?	1	NA	NA	NA	NA	6	0	1	1	10–22	9	R	9.0	(86.5)
Psychoglypha	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Psychoronia	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Pycnopsyche	0?	9	6	3	6	0	6	0	1	1	16–23	3	R	17.5	(65.0)
Philopotamidae	3?	9	1	1	3	3	6	3	1	1	10–14	9	C	48.0	(31.5)
Polycentropodidae	3	9	1	1	6	3	6	3	1	1	20–28	3	C	44.4	37
Psychomyiidae	3?	9	1	1	3	3	6	3	1	1	4–8	9	R	20.0	(57.5)
Rhyacophilidae	0?	9	6	3	3	3	6	3	1	1	11–18	9	C	52.8	17.0
Uenoidae	0?	9	6	3	3	0	6	3/0	1	1	10–14	9	C	49.2	(26.5)
Diptera															
Athericidae	0?	9	6	3	6	6	3	0	6?	1	12–18	9	C	58.8	13.0
Blephariceridae	0?	9	1	1	1	6	6	0	6	3	5–10	9	R	21.0	54
Ceratopogonidae	0?	1	NA	NA	NA	NA	6	6?	6	1	1–5	3	R	11.5	(82.0)
Chironomidae (free-living)	0?	9/1	0	3	1	6	6	6/3	6/1	1	2–8	9	A	70.5	4
Orthocadiinae															
Cardiocladius	0?	9	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Cricotopus	0?	9/1	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Tanytarsini	0?	9/1	1	1	1	6	6	6/3	6	1	2–5	3	C	48.0	(31.5)
Deuterophlebiidae	0?	9	1	3	1	6	6	3?	6	3	3	3	R	20.5	55.0
Dixidae	0?	1	NA	NA	NA	NA	3	0	6	1	2–5	3	R	7.0	(91.5)
Empididae	0?	9/1	0	3	1	6	6?	6?	6?	1	2–7	3	C	49.2	(26.5)
Muscidae	0?	9	0	3	3	6	3?	3?	6	1	6–10	9	R	21.5	(52.0)
Psychodidae															
Maruina	0?	9	1	3	1	6	3?	3?	6	3	2–5	3	C	45.6	(35.5)
Pericoma	0?	1	NA	NA	NA	NA	6?	6?	6	1	2–5	3	R	11.5	(82.0)
Simuliidae	9	9	6	1	1	3	6	6/0/3	6	3	1–5.5	3	A	79.5	2.0

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Table 5. (*concluded*).

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior	Ovipositing behavior	Diel activity	Benthic exposure	Size (mm)	Size scores	Abundance	Total	Rank
Stratiomyidae	0?	9	0	3	1	6	6	0	6?	1	2–18	3	R	17.5	(65.0)
Tabanidae	0?	1	NA	NA	NA	NA	3?	0	6	1	10–50	3	R	7.0	(91.5)
Tanyderidae	0?	9?	0	3	3	6	3?	3?	6	1	8–14	9	R	21.5	(52.0)
Tipulidae															
Antocha	0?	9	0	3	6	6	3?	0	6	1	12–24	9	C	51.6	(20.0)
Dicranota	0?	9	0	3	6	6	3?	0	6	1	12–24	9	C	51.6	(20.0)
Hexatoma	0?	1?	NA	NA	NA	NA	3	0	6	1	30–60	3	R	7.0	(91.5)
Limnophila	0?	1?	NA	NA	NA	NA	3	0	6	1	20–40	3	C	10.0	(85.0)
Limonia	0?	9?	0	3	6	6	3	0	6	1	10–22	9	C	51.6	(20.0)
Pedicia	0?	9	0	3	6	6	3	0	6	1	10–22	9	C	51.6	(20.0)
Rhabdomastix	0?	1	NA	NA	NA	NA	3	0	6	1	12–24	9	R	10.0	(85.0)
Tipula	0?	1	NA	NA	NA	NA	3	0	6	1	30–60	3	R	7.0	(91.5)
Coleoptera															
Dryopidae	0?	9	6	3	1	3	NA	NA	NA	1	4–10	9	C	34.0	(40.5)
Elmidae	0?	9	6	3	1	3	3	3	NA	1	2–8	3	C	34.0	(40.5)
Psephenidae	0?	9	1	1	1	6	3	3	1?	1	3–6	3	R	14.5	(72.0)
Odonata	3?	1	NA	NA	NA	NA	3	6	6	1	>10	9	R	14.5	(72.0)
Lepidoptera															
Petrophila	3?	9	1	1	6	3	6	3	1	1	11–25	9	R	21.5	(52.0)
Megaloptera															
Corydalidae	0?	9	6	3	6	3	3	0	6?	1	40–80	3	R	20.0	(57.5)
Sialidae	0?	9	6	3	6	3	3	0	6?	1	16–26	3	R	20.0	(57.5)
Collembola	0?	1	NA	NA	NA	6	NA	NA	NA	NA	<1.0	1	C	8.0	(89.0)
Oligochaeta	0?	1	NA	NA	NA	NA	NA	NA	NA	0	2–20	9	C	10.0	(85.0)
Turbellaria	0?	9	6	3	1	6	NA	NA	NA	1	5–10	9	C	42.0	(38.5)
Amphipoda	9?	9	6	9	6	1	NA	NA	NA	3	5–12	9	C	62.4	(9.5)
Gastropoda															
Snails	0?	1	NA	NA	NA	NA	NA	NA	NA	1	4–12	9	C	13.0	75.0
Pelecypoda	0?	1	NA	NA	NA	NA	NA	NA	NA	0	2–8	3	R	2.0	95.0

Note: A question mark and NA indicate uncertain designations based on closely related taxa and categories that were not applicable. A solidus separates scores where multiple designations apply. The first score was used to calculate the total and rank. A, C, or R indicate Abundant, Common, or Rare taxa, respectively. Parentheses indicate shared ranks.

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Fig. 2. Association between the predicted ranks versus the actual percent abundance (average number of individuals per gut) of macroinvertebrates from (*a*) brook trout and (*b* and *c*) cutthroat populations using data from Allan (1978), Bozek et al. (1994), and Young et al. (1997).

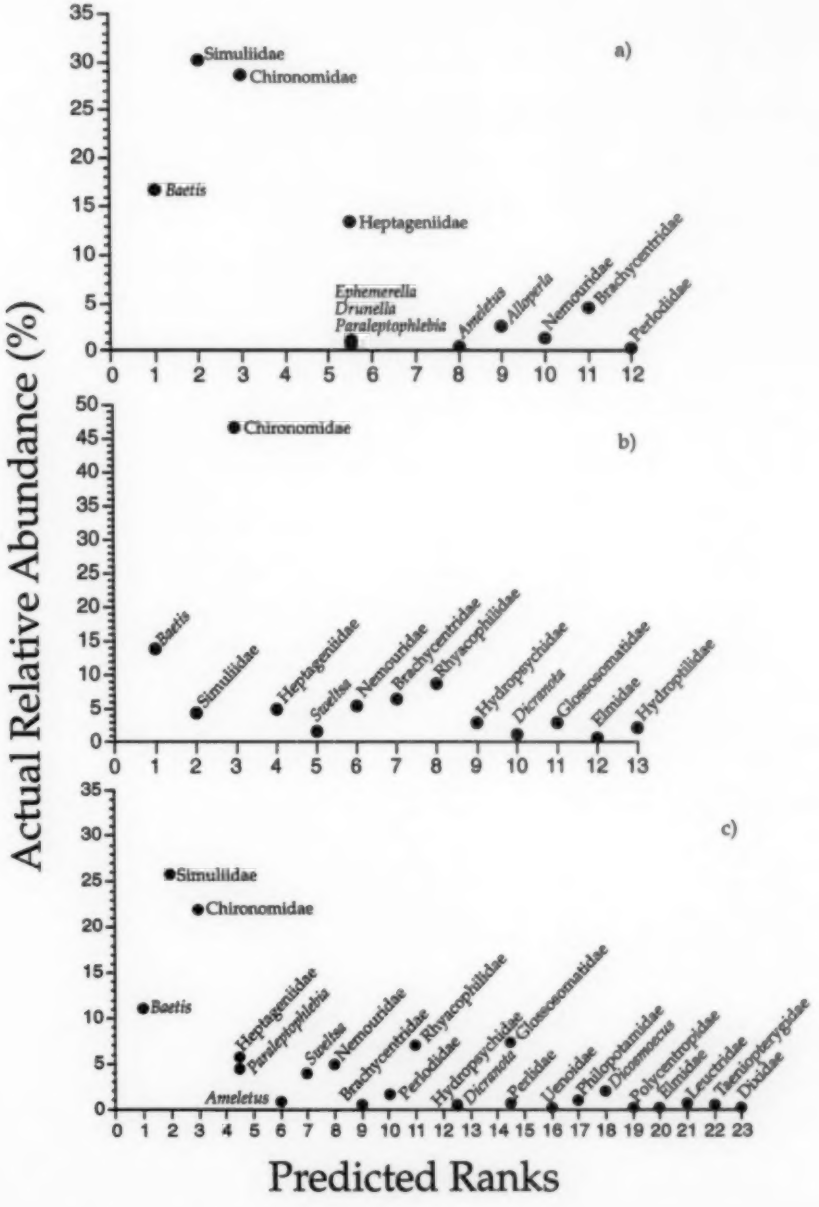

Table 1. Both the cluster analysis and ranking procedure were also used to classify taxa into drift groups based only on the first six categories of Table 1 (Intentional Drift, Habitat, Flow Exposure, Mobility, Drag Index, and Drift Distance).

Results

When stream invertebrates were ranked according to their availability based on the total of category scores (including Abundance as a multiplier), they separated into *Baetis* and three groups (Table 5). *Baetis* was the highest ranked taxon with a score 13.5 points higher than the next highest ranked taxa, Simuliidae. The Simuliidae, *Acentrella*, and free-living Chironomidae were separated by 4 or fewer points and comprised the first group. The second availability group started with the Heptageniidae, *Paraleptophlebia*, *Ephemerella*, and *Drunella* (tied ranks) and gradually decreased (consecutive taxa were separated by 1 point or less) through an additional

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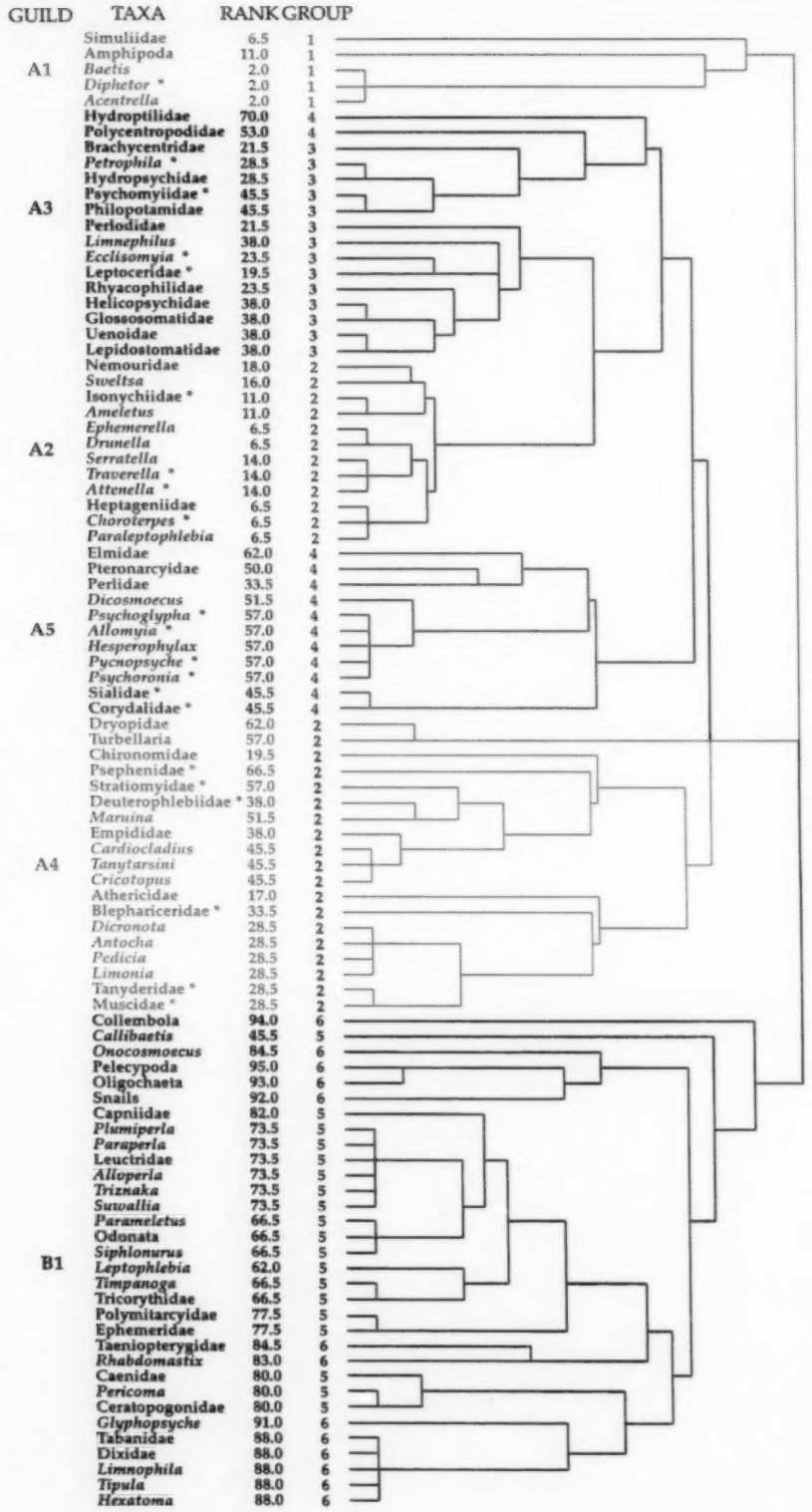

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Fig. 3. Cluster dendrogram (hierarchical technique) showing the classification of 95 taxa into five availability groups (A1–A5) and one relatively unavailable group (B1). Values in the rank column identified the rank availability of each taxa as a food resource for salmonids (see text for a complete description). The ranking procedure and cluster analysis were based on the traits in Table 1 excluding abundance. When abundance was included as a multiplier used to modify availability scores, taxa with an asterisk were given a Rare designation for streams in the subalpine and montane zones of the central Rocky Mountains and comprised a second unavailable group.

32 taxa. The third and least available group started with the beetles (Elmidae and Dryopidae) and declined in score (1 point or less separated consecutively ranked taxa) through 56 taxa until reaching the Pelecypoda. Gaps of 7 and 8 points separated group 1 from 2 and group 2 from 3, respectively. Sixty-one percent of the taxa occurred in the least available group (group 3). The most highly ranked taxa (in descending order) of the most diverse orders were (*i*) *Baetis*, *Acentrella*, Heptageniidae, *Paraleptophlebia*, *Ephemerella*, and *Drunella* (Ephemeroptera), (*ii*) Simuliidae and free-living Chironomidae (Diptera), (*iii*) *Sweltsa*, Nemouridae, Perlodidae, and Perlidae (Plecoptera), and (*iv*) Brachycentridae, Rhyacophilidae, and Hydropsychidae (Trichoptera).

Predicted ranks were significantly correlated with the actual rank of macroinvertebrates in trout guts from each of the three studies examined (Fig. 2). Spearman's correlation coefficient (r) was 0.61 ($P = 0.018$), 0.66 ($P = 0.008$), and 0.70 ($P = 0.0001$) for data from Allan (1978), Bozek et al. (1994), and Young et al. (1996), respectively. These results suggested that this index was proficient at predicting the rank of macroinvertebrates occurring in gut samples from specific streams. All taxa, except Hydroptilidae (Bozek et al. 1994), Leuctridae, Dixidae, and Taeniopterygidae (Young et al. 1997), occurred in the top two highest ranked availability groups. Out of a total of 48 taxa (gut samples from all three studies), these four taxa were represented by a single individual and were ranked in the lowest availability group. The most abundant taxa in guts from each study (Fig. 2) always occurred in the highest ranked group. The ranking procedure predicted which taxa would occur in trout stomachs and their rank order of abundance.

Based on benthic samples collected from each site, several taxa with predicted high availability were absent from trout guts. In particular, *Rhithrogena* spp. (Heptageniidae), *Pteronarcella badia* (Pteronarcyidae), and *Rhyacophila* spp. (Rhycophilidae) were common in the benthos but absent from brook trout guts in Cement Creek, Colorado (Allan 1978). Similarly, Perlodidae, Perlidae, *Ephemerella* spp., and *Drunella* spp. were common in the benthos but absent from cutthroat gut samples in the North Fork of the Little Snake River (Bozek et al. 1994; Young et al. 1997). Either the index has exaggerated the importance of these taxa as a food resource for trout or their absence from these gut examinations was a result of sampling deficiency. Since these taxa were commonly consumed by trout in other studies (e.g., Tusa 1968; Griffith 1974; Skinner 1985), their absence was probably due to sampling deficiencies.

The cluster analysis (abundance excluded) accounted for 65% of the variation (n-dimensional space) in the assignment of taxa into groups. Both hierarchical and nonhierarchical techniques assigned taxa to similar clusters. Therefore, only results from the hierarchical technique (dendrogram) are shown (Fig. 3) and the nonhierarchical technique is used to provide R^2 values. The cluster analysis separated stream invertebrates into six groups or proposed guilds based on their availability to salmonids in the Rocky Mountain Region (Fig. 3). Results from the rankings procedure corresponded to results from the cluster analysis. Similarly ranked taxa clustered into the same groups (Fig. 3). The rankings of individual taxa were used to determine the relative availability of each guild (A1 > A2 > A3 > A4 > A5 > B1).

Habitat ($R^2 = 0.996$) separated taxa into two groups (A and B). Taxa in the A group inhabited riffles whereas taxa in the least available group (B) inhabited either the hyporheic zone or depositional areas. Mobility ($R^2 = 0.758$), Intentional Drift ($R^2 = 0.681$), Drift Distance ($R^2 = 0.663$), Drag Index ($R^2 = 0.574$), Flow Exposure ($R^2 = 0.554$), Adult Diel Activity ($R^2 = 0.562$), and Ovipositing Behavior ($R^2 = 0.553$) were all important in separating taxa of the A group into five clusters (Fig. 3). Benthic Exposure ($R^2 = 0.432$) and Size ($R^2 = 0.428$) were somewhat less important because they were only influential in separating a few taxa into their respective clusters. Emergence Behavior ($R^2 = 0.183$) was the only category that appeared to have little influence on the separation of taxa into guilds.

In addition to inhabiting the hyporheos and depositional areas, taxa in B1 dig burrows and bury themselves in fine sediment. All taxa in the most available guild (A1) were swimmers (except Simuliidae) and frequent intentional drifters in the facultative Flow Exposure category. Other swimmers (e.g., *Callibaetis*, *Parameletus*, *Siphlonurus*, *Leptophlebia*) inhabited depositional areas or clustered into the A2 guild (Isonychiidae, *Paraleptophlebia*, *Ameletus*). Guilds A3 and A5 were primarily composed of the most and least available Trichoptera, respectively. Size was the primary difference. Trichoptera in the A3 guild were closer to the more available intermediate size class whereas A5 Trichoptera were either too small or too large. Riffle dwelling stoneflies (Perlodidae, Nemouridae, *Sweltsa*, Pteronarcyidae, Perlidae) were dispersed among three guilds (A2, A3, and A5). Size was again important, as Pteronarcyidae and Perlidae (A5) were large and considered difficult to handle. Nemouridae and *Sweltsa* (A2) had day-active adults whereas Perlodidae (A3) were nocturnal. Taxa in the A4 guild were composed of the most available, riffle-dwelling dipterans that were crawlers with a high drag index and would passively float once dislodged. Most dipterans in A4 also had day-active adults.

The primary affect of including abundance as a factor in the cluster analysis was to create a second relatively unavailable guild (B2). Twenty-one riffle-dwelling taxa from the A group were assigned a Rare designation which added them to the less available B group. These taxa are identified with an asterisk in Fig. 3. All total, 56% or 53 taxa (B1 + B2) comprised the relatively unavailable B group; rare riffle-dwelling taxa and taxa that inhabit depositional areas or the hyporheos. Including abundance also added the Chironomidae to the most available guild (A1) because it clustered with *Baetis* and the Simuliidae which were also given an Abundant designation.

The final objective was to propose a functional classification of the drift based on the first six categories in Table 1. For amphibiotic aquatic insects, this is a functional classification of immature stages since adult traits were excluded. When

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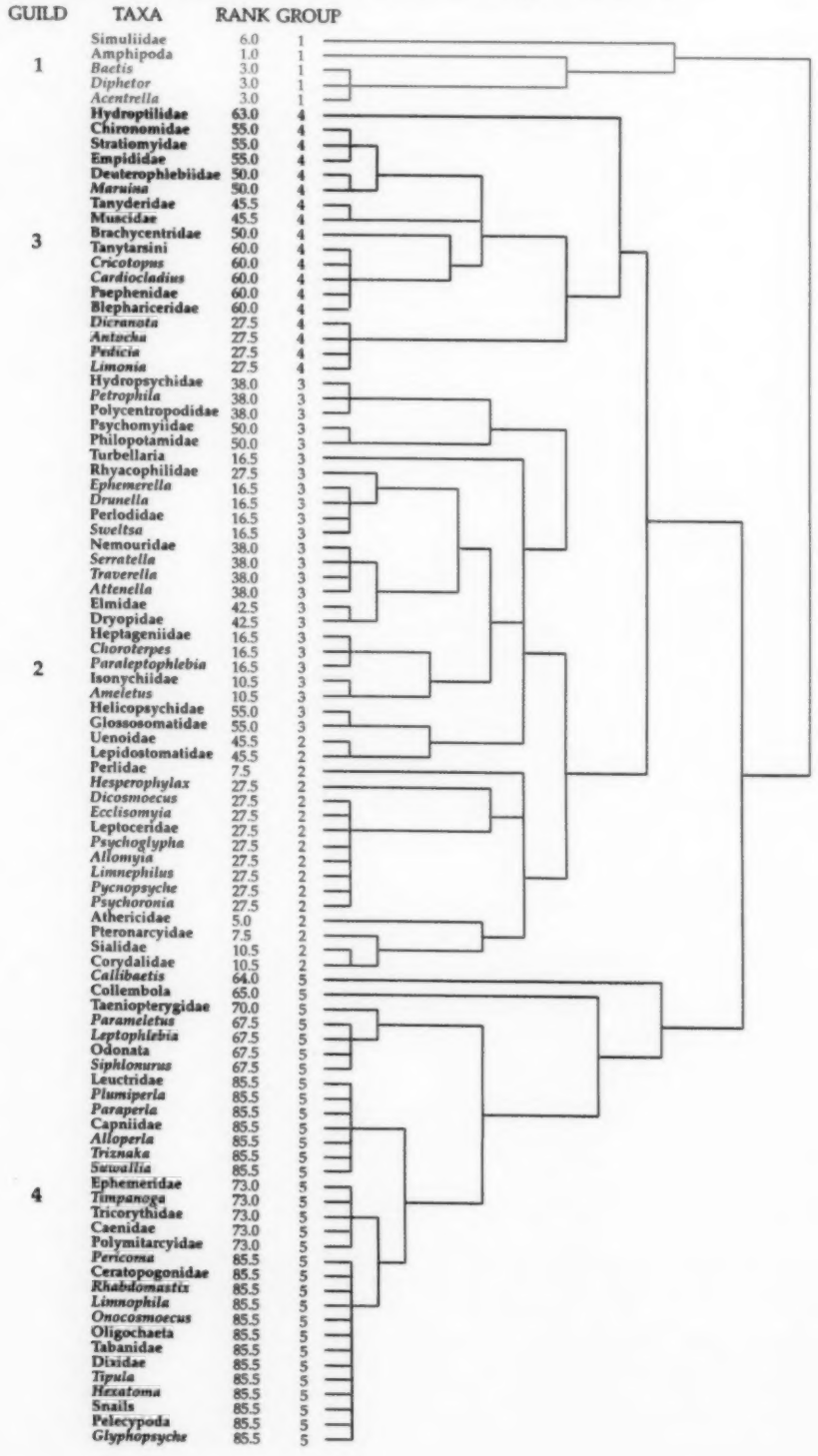
Fig. 4. Cluster dendrogram (hierarchical) showing the classification of 95 taxa into four guilds with similar propensities to drift based on six traits (Intentional Drift, Habitat, Flow Exposure, Mobility, Drag Index, and Drift Distance). Values in the rank column identify the drift rank of each taxon based on its total score using the first six traits of Table 1 (see text for complete descriptions).



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stream invertebrates were ranked using the sum of category scores, which was a measure of their propensity to drift (intentional and accidental), they separated into Amphipoda and three groups. Amphipods were the highest ranked taxa with a score 5.0 points higher than group 1. Group 1 was composed of three taxa (*Baetis*, *Acentrella*, *Diphetor*) with tied ranks and was 5.0 points greater than the much larger group 2. Group 2 started with the Simuliidae and gradually decreased (consecutive taxa were separated by no more than 2 points) through an additional 57 taxa. The third and least likely group to drift started with *Callibaetis* and declined in score (1 point or less separated consecutively ranked taxa) through 33 taxa. A gap of 7 points separated group 2 from group 3. Taxa in group 3 should have a low propensity to drift.

The cluster analysis assigned taxa into four guilds based their propensity to drift (Fig. 4). The cluster analysis accounted for 86% of the variation in the assignment of taxa into guilds. As in the availability cluster analysis, invertebrate rankings corresponded to the results from the cluster analyses (i.e., similarly ranked taxa clustered into the same groups). Based on this analysis, the propensity to drift was greatest in guild 1 and decreased through guilds 2 and 3 to the least likely group of taxa to drift, guild 4 (Fig. 4).

Three variables (Habitat, $R^2 = 0.996$; Flow Exposure, $R^2 = 0.993$; Mobility, $R^2 = 0.800$) were most important in controlling the clustering of taxa into drift guilds. All members of guild 4 inhabited depositional or hyporheic habitats whereas all taxa in guilds 1, 2, and 3 were classified in the Riffle subcategory. Except for the Simuliidae, all taxa in guild 1 were swimmers with a frequent propensity to intentionally drift and were classified as Facultative in the Flow Exposure category. Simuliidae shared the same traits with the rest of the taxa in guild 1 except they were assigned to the Attached mobility subcategory. All six variables, including Intentional Drift ($R^2 = 0.661$), Drag Index ($R^2 = 0.691$), and Drift Distance ($R^2 = 0.670$), were important in assigning and clustering taxa into guilds 2 and 3. Guild 2 was composed of riffle-dwelling mayflies, stoneflies, and caddisflies (free-living, net-spinning, case-making, tube-dwelling). Except for Psephenidae, Brachycentridae, and Hydroptilidae, taxa in guild 3 were primarily riffle-dwelling dipterans.

A comparison of drift and availability revealed that the guild with the greatest propensity to drift (*i*) was identical to the guild with the greatest availability to salmonids (A1) (Figs. 3 and 4). Similarly, the guild with the least propensity to drift (4) was identical to the group with the lowest availability (B1). Except for Hydroptilidae and Brachycentridae (A3), drift guild 2 included availability guilds A2, A3, and A5 and three difficult taxa to classify (Athericidae, Dryopidae, Turbellaria) from A4. Except for these three taxa, A4 was identical to drift guild 3. The A5 group was one of the least available groups to salmonids because of size and adult characteristics, not because of their drift propensity because they were part of the second most likely group to drift (2).

Discussion

The ability of this model to predict differences in drift and availability among groups of taxa with different traits depends on (*i*) identifying the important traits, (*ii*) understanding their relationship to drift and availability, and (*iii*) gathering sufficient trait information on taxa for accurate classification. The traits chosen for this analysis and invertebrate classification fall into five groups: intentional, accidental and adult drift propensity, exposure on the stream bottom, and body size. Intentional drift propensity is a behavioral trait whereas accidental drift, adult drift, benthic exposure, and body size incorporate both behavioral and morphological characteristics. Many more traits were considered than were included in this analysis. Some traits (e.g., functional feeding groups) were excluded in favor of morphological and behavioral attributes that could better define the propensity to drift. For example, Hydroptilidae and *Baetis* are both grazers but they have very different drift propensities. Differences in drift are likely determined by different morphological and behavioral traits (facultative flow exposure, streamlined, swimmers versus obligate flow exposure, attached, case-makers) and is only indirectly related to mouth part morphology and the consumption of algae. Other potentially important traits were considered but could not be included because of a lack of information (e.g., ability of adults to quickly break the surface tension of the water and fly away, adult tendency to swarm, life cycle synchrony). Waters (1968) found that the drift of a rock-cased caddisfly (*Oligophlebodes sigma*) in a trout stream in Utah peaked during the day when temperatures were highest. This day-active pattern is opposite from many species whose drift peak occurs at night. To the extent that future research reveals this behavior to be typical of other caddisflies, day-active, temperature-dependent drift might be an important trait that will influence availability and should be included in future classification efforts. More information is also needed for some traits included in this analysis. This study represents the first attempt to characterize the intentional drift propensity of stream invertebrates. Although stream ecologists have long recognized that stream invertebrates could, for a variety of reasons, intentionally release their hold on the substrate and drift downstream (Waters 1972), it was not until the recent emphasis on behavioral observations (e.g., Peckarsky 1980) that such empirical data were available. However, adequate information on intentional drift frequencies has only been determined for five genera (*Baetis*, *Ephemerella*, *Paraleptophlebia*, *Prosimulium*, and *Simulium*). Further research on the intentional drift frequency of other taxa is required. A better understanding of how each trait influences invertebrate drift and availability will also increase predictability. Differences between subcategory scores should be determined by the relationship (linear, quadratic, etc.) between a particular trait and availability. Although the general direction of the relationship (positive or negative) was known for all traits or categories, the specific shape (a straight line was assumed for most traits) was only known for a few categories (e.g., Drift Distance). For example, "Passive Floaters" are known to drift five or six times farther than invertebrates that actively swim to exit the drift (Elliott 1971). For most categories, however, there were no data to indicate appropriate differences between subcategory scores. In the absence of data relating flow exposure groups to dislodgment, "Facultatives" were arbitrarily assigned a three times greater score than "Obligates." Future research should clarify relationships between each category/trait and drift/availability to provide more accurate information on differences among subcategory scores.

Predicting differences in availability among groups of aquatic taxa with different traits is the first step in predicting

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the actual food or energy available for salmonid growth and reproduction. Actual available energy depends on: (*i*) abundance and species composition of the aquatic invertebrate community, (*ii*) abundance and species composition of the terrestrial invertebrate community, (*iii*) abundance of vertebrate prey (e.g., amphibians, mice, and small fish), and (*iv*) the environmental attributes that influence the availability of the first three factors (e.g., density of riparian vegetation). This study has investigated the relationship between food availability and the species composition of the benthic community by exploring traits that influence drift and availability of specific taxa. Future research should include the terrestrial invertebrate component and the environmental factors that influence the amount of both aquatic and terrestrial inputs as part of a model to estimate total energy available for salmonid production.

A simple equation can be used to express the aquatic species component of a larger model for predicting actual food availability for salmonids. The contribution of the aquatic species composition (ASC) can be calculated as

$$\mathrm{ASC} = \sum_{i=1}^{n} (\mathrm{St}_i \cdot A_i)$$

where n is the number of taxa in availability guilds A1–A5 (Fig. 3). St is an availability factor based on classifying each taxon according to the traits found in Table 1 and is the subtotal score (sum the subcategory scores for each taxa) from Table 5 (abundance excluded). A is an abundance factor. How it is calculated depends, in part, on the spatial scale. Patterns at large scales (comparisons in food availability across regions, basins, and watersheds) may be best detected with coarse-grained data (Margalef 1968). Therefore, at larger scales, presence–absence data based on qualitative sampling techniques could be used to identify the taxa in guilds A1–A5 and A becomes a multiplier (0.5, 1.0, 1.2, 1.5) used to modify St. Also, information on large-scale patterns of relative abundance could be gathered from the literature (e.g., regional keys), in addition to qualitative samples, and used to separate taxa into abundance categories (rare, common, and abundant). The choice of a multiplier depends on the abundance category and if the taxa have an availability score greater than or less than the mean St (see Methods for a complete description). At smaller scales (stream reaches and habitat units), pattern detection may require fine-grained data (quantitative estimates of population density). For small-scaled predictions, St for each taxon could be multiplied by density estimates based on quantitative benthic samples. This equation used at large or small scales (using coarse-grained or fine-grained data) provides a single value expressing relative food availability of aquatic invertebrates for salmonids based on a relatively simple level of taxonomic resolution (primarily family with some genus identifications).

This investigation and invertebrate classification has a variety of potential uses related to the transfer of energy from lower to higher trophic levels. Both natural and anthropic disturbances can alter macroinvertebrate community structure, causing some taxa to decrease whereas the abundance of others might remain unchanged or even increased (e.g., effects of eutrophication). This study provides specific criteria for determining when alterations in invertebrate community structure will affect food resources for higher trophic levels by causing a decline in the most available taxa. The relationship between total invertebrate production and salmonid production is not a positive, linear function. Increased production of unavailable taxa may have little or no impact on salmonid production. Similarly, if species were deleted from the community, the function of transporting energy from lower to higher trophic levels may or may not be altered. The relationship between community diversity and ecosystem function (transfer of energy to higher trophic levels; Lawton 1994) may depend on the availability of the deleted taxa. That is, ecosystem function will decline as available taxa are deleted. This research also supports previous findings that floods are important in maintaining invertebrates that represent an important food resource for salmonids (Power et al. 1996). Taxa that were efficient at exploiting recently disturbed habitats (Power et al. 1996) were identified in this study as being the same taxa that are most available to salmonids (e.g., mayflies in guilds A1 and A2). The least resilient taxon (*Dicosmoecus*), which when abundant can suppress algal resources and mayfly populations, was assigned to one of the guilds with the lowest availability (A5). Hemphill and Cooper (1983) also found an increase in the abundance of *Simulium virgatum* (Simuliidae) and a decrease in *Hydropsyche oslari* (Hydropsychidae) as disturbance frequency increased. Hart (1987) suggested that disturbances might prevent the competitively superior species (*H. oslari*) from excluding the "fugative" species (*S. virgatum*). My results indicate that Simuliidae (group A1) possess traits that make them more available to salmonids than Hydropsychidae (group A3). Both studies (Hemphill and Cooper 1983; Power et al. 1996) suggest that traits that enhance recovery from disturbances may also increase availability to salmonids. Combining the availability traits of this research with life history traits that determine resilience to physical disturbance (growth rate, generation time, dispersal capability) may help to define the role of disturbances in maintaining invertebrates that are important in maintaining salmonid populations. In addition to being an important fish food, invertebrates can also be used as a biomonitoring tool to assess the health of stream ecosystems (Rosenberg and Resh 1993). However, drift can carry invertebrates from unimpacted upstream areas into downstream impacted sites creating the false perception of a healthy environment. Knowledge of the drift propensity of specific taxa (drift guilds 1 and 2 versus 3 and 4) can be valuable in separating taxa that seldom drift from frequent drifters that might temporarily occur in the benthos but are not indicative of localized impacted conditions.

This study was specific to trout streams of the subalpine, montane, and foothills zones of the central Rocky Mountains. Invertebrate classification was based on traits specific to taxa that reside within this ecoregion. Although taxa in other ecoregions may be classified differently from taxa in the Rocky Mountains, the traits/categories/criteria found in Table 1 can be used to rank and classify taxa in trout streams from all ecoregions. Similarly, the ranking and classification of taxa in this study was based on their importance as a food resource for juvenile and adult trout. Gape-limited YOY trout that forage in side channels, backwaters, and stream margins primarily rely upon smaller aquatic insects and microcrustaceans as a food resource (Shiozawa 1986; Hubert and Rhodes 1992). A separate set of criteria is necessary to rank and classify invertebrates based on their importance to YOY trout.

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This study is an investigator-defined, a priori classification of stream invertebrate taxa into both drift and availability guilds using specifically defined criteria (traits or categories of Table 1) and objective clustering techniques. The predictive power of this model depends on the degree that these guilds represent real ecological units. Although a preliminary analysis comparing the predicted with the actual rank of taxa in salmonid guts suggests that these guilds may represent real ecological units, future research should expand upon this test and compare the predicted rankings to a larger data set including both drift and trout gut analyses in the Rocky Mountains.

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Changes in life history parameters in a naturally spawning population of chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish

M.J. Unwin and G.J. Glova

Abstract: Chinook salmon (*Oncorhynchus tshawytscha*) spawning runs in Glenariffe Stream, New Zealand, exhibited significant changes in life history traits following supplementation releases of hatchery-reared juveniles. Total run strength did not change but the proportion of naturally produced fish declined to 34%. Attempts to separate spawners of natural and hatchery origin were unsuccessful, and 31–48% of natural spawners are now of hatchery origin. Hatchery males were smaller at age 2 and 3 than males of natural origin, and more often matured as jacks, producing an 86-mm decrease in mean fork length over 28 years. There was no change in length at age or age at maturity for female spawners. The proportion of jacks entering Glenariffe Stream each year was positively correlated with the proportion of jacks in the ensuing cohort. Most differences between fish of natural and hatchery origin were related to hatchery rearing practices, but the decline in age at maturity among naturally produced males appears to reflect traits inherited from parent stock of hatchery origin. Hatchery releases may also favour the survival of ocean-type fry over stream-type fry, possibly reversing a tendency for stream-type behaviour to evolve in response to the lack of estuaries on most New Zealand chinook salmon rivers.

Résumé : Les caractéristiques du cycle vital du saumon chinook (*Oncorhynchus tshawytscha*) participant aux montaisons de reproduction dans le ruisseau Glenariffe, en Nouvelle-Zélande, ont subi des changements importants après la libération de juvéniles élevés en écloserie pour renforcer la population. L'effectif total de la montaison n a pas changé, mais la proportion de poissons produits naturellement a décliné à 34 %. Les tentatives pour séparer les reproducteurs d'origine naturelle des reproducteurs provenant de l'écloserie ont échoué et 31–48 % des reproducteurs naturels proviennent maintenant des stocks d'élevage. Les mâles d'élevage sont de plus petite taille aux âges de 2 et 3 ans que les mâles d'origine naturelle et ils arrivent plus souvent à maturité à l'état de jeunes mâles précoces, ce qui donne une diminution de 86 mm de la longueur moyenne à la fourche en l'espace de 28 ans. Il n y a pas de changement pour ce qui est de la longueur selon l'âge et l'âge à maturité pour les femelles reproductrices. La proportion de jeunes mâles précoces faisant leur entrée dans le ruisseau Glenariffe chaque année présentait une corrélation positive avec la proportion de jeunes mâles précoces dans la cohorte suivante. La plupart des différences entre les poissons d'origine naturelle et les poissons d'élevage sont liées aux pratiques d'élevage en l'écloserie, mais le déclin dans l'âge à maturité observé chez les mâles d'origine naturelle semble refléter des caractères hérités du stock parental provenant de l'élevage. L'élevage pourrait également favoriser la survie des alevins océaniques par rapport à celle des alevins de cours d'eau, peut-être en inversant la tendance du comportement de cours d'eau à évoluer en réaction à l'absence d'estuaires dans la plupart des rivières à saumon chinook de la Nouvelle-Zélande.
[Traduit par la Rédaction]

Introduction

Over the last 10–15 years, concern about possible adverse effects of hatchery-reared salmonids on wild stocks has become increasingly widespread, both in the Pacific Northwest (Helle 1981; Waples 1991; Thomas and Mathisen 1993) and in Scandinavia and the United Kingdom (Ryman and Stahl 1981; Crozier 1993; Heggberget et al. 1993). A recurrent theme in these reports is the potential for detrimental effects on the gene pool, because of inbreeding in hatchery stock (which may result in reduced genetic diversity) or interbreeding in naturally spawning populations between fish of wild and hatchery origin (which may yield offspring with reduced fitness to survive, e.g., Hindar et al. 1991; Waples 1991). There is also concern about impacts on wild stocks through increased competition from hatchery fish (Cooney 1993; Hilborn and Winton 1993). These issues have led to a lively and continuing debate on the value of hatchery supplementation programmes such as Canada's Salmonid Enhancement Programme (SEP) (Hilborn 1992; Washington and Koziol 1993; Winton and Hilborn 1994), although there is wide agreement that hatcheries have an important role to play provided their operations are properly managed (Waples 1991; Brannon 1993; Fleming 1994).

Many life history traits in salmonids are under some measure of genetic control (e.g., age at maturity (Ricker 1972; Hankin et al. 1993) and run timing (Siitonen and Gall 1989; Hansen and Jonsson 1991)) and could readily be influenced by

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hatchery practices. Specific traits for which phenotypic and (or) genetic differences between wild and hatchery salmonids have been demonstrated include growth and survival rates in steelhead trout (*Oncorhynchus mykiss*) (Reisenbichler and McIntyre 1977) and body morphology, reproductive potential, and rates of aggressive display in coho salmon (*Oncorhynchus kisutch*) (Taylor 1986; Swain and Riddell 1990; Swain et al. 1991; Fleming and Gross 1992). However, there is virtually no information available on the extent to which interactions between wild and hatchery salmonids have actually affected wild stocks (Winton and Hilborn 1994).

Chinook salmon (*Oncorhynchus tshawytscha*) were introduced to New Zealand from fall-run Sacramento River stock in the early 1900s (McDowall 1995) and had established self-sustaining populations on the east coast of the South Island by about 1915. Hatchery releases largely ceased by the mid-1920s, and the fishery was maintained solely by naturally spawning stocks until about 1980. Studies of chinook populations in the Rakaia River and a spring-fed tributary, Glenariffe Stream (where a counting fence has been maintained since 1965), have confirmed that New Zealand stocks are essentially fall-run (Flain 1982; Unwin 1986; Hopkins and Unwin 1987) but include both stream- and ocean-type life histories (Gilbert 1913; Healey 1983; Unwin and Lucas 1993). Phenotypic differences between populations in various New Zealand rivers (Quinn and Unwin 1993) and biochemical genetic comparisons between representative New Zealand and present-day Sacramento populations (Quinn et al. 1996) indicate that some degree of adaptation to New Zealand conditions has taken place over a period of 25–30 generations.

In the late 1970s, increasing interest in commercial salmon farming led to reestablishment of hatcheries on many New Zealand salmon rivers (Beckett 1981; Crowe 1985; McDowall 1990). These developed slowly until about 1983, with a total annual output of 1–2 million fry, but expanded rapidly from 1984 to 1987, with a peak output of 6.6 million fry in 1987 (Unwin 1991). To provide research backing and a guaranteed supply of stock for the developing industry, the New Zealand Government (through the Ministry of Agriculture and Fisheries) established hatchery facilities at Glenariffe Stream in 1978. Releases from the 1978 spawning began in January 1979, and the first returning adults appeared in 1980.

Data from the Glenariffe Stream counting fence now provide a continuous record of annual spawning runs from 1965 to 1994, the last 15 of which have been associated with increasing returns of hatchery-reared chinook. The objective of this study was to determine the impact of hatchery-released chinook on the spawning population in Glenariffe Stream by assessing trends in annual run strength and phenotypic characters associated with key life history traits. Specifically, we tested the null hypotheses that there had been no long-term trends in (*i*) run strength, (*ii*) age at maturity, (*iii*) length at age, and (*iv*) run timing, for adult chinook of natural and hatchery origin, over the period 1965–1994. In this context, and throughout this paper, the terms "natural" and "naturally produced" refer to all progeny of naturally spawning parents, irrespective of whether one or both parents were of natural or hatchery origin.

Study area

Glenariffe Stream is one of four major chinook salmon spawning tributaries in the upper Rakaia River, joining the latter 98 km above the river mouth at an altitude of 430 m. It flows through open flats covered in coarse native grasses and uncultivated pasture, adjacent to the main Rakaia River flood plain, with a total length of 22 km in four main branches. The stream is primarily spring fed with a mean discharge of about 4 $m^3 \cdot s^{-1}$. Water temperatures average 7–9°C in winter and 10–16°C in summer (Unwin 1986). The counting fence is located approximately 100 m above the Glenariffe/Rakaia confluence (Flain 1982; Quinn and Unwin 1993). This fence spans the stream and thus provides a complete count of chinook spawning above the fence site (see Unwin (1986) for a location map). From 1965 to 1978, an average of 1920 chinook spawned in Glenariffe Stream (Flain 1982), with peak spawning in late April (Quinn and Unwin 1993). Fry emergence takes place from August to October, with most fry (90–99%) entering the Rakaia River within 24 h of emergence (Unwin 1986). Subsequently, ocean-type fry typically rear for 3–6 months in the Rakaia River, gradually moving downriver, and enter the ocean from November to January (Hopkins and Unwin 1987; Unwin and Lucas 1993). Stream-type fry remain in Glenariffe Stream and (or) the Rakaia River until the following spring, entering the sea as yearlings (Unwin 1986; Quinn and Unwin 1993; Unwin and Lucas 1993).

Hatchery operation

Rearing facilities, consisting of four concrete raceways, were constructed at the fence site on Glenariffe Stream in 1978, with further raceways added in 1982 and 1987. These were supplied by a diversion canal from a small tributary of Glenariffe Stream 1 km upstream. The raceway outfall (and hence the release point for all hatchery fish) discharges into Glenariffe Stream just above the Glenariffe/Rakaia confluence, 50 m below the counting fence and thus well below all the main spawning and rearing areas. The increasing volume of water diverted through the raceways after the 1987 expansion resulted in large numbers of adult chinook attempting to return directly up the raceway outfall. To alleviate this problem, and (it was hoped) to allow adults of natural and hatchery origin to be trapped independently, a second upstream trap was established on the outfall.

The hatchery was supplied exclusively with gametes from 3- and 4-year-old adult chinook returning to Glenariffe Stream and intercepted at the counting fence. Once returns of hatchery-reared adults became established, individuals identifiable as being of hatchery origin (e.g., by a missing adipose fin as described below) were used as broodstock whenever possible. Surplus jacks were culled, but all other fish surplus to ova requirements were released into Glenariffe Stream above the counting fence. Until 1986, eggs were incubated in Washington pond trays (Senn et al. 1973) submerged in the hatchery raceways, covered in black polythene sheeting to maintain darkness. In 1987, this system was replaced by a more conventional hatchery, comprising incubation and trough rearing facilities fed by pumped groundwater at 6–11°C. Incubators were constructed from 20-L plastic pails, with a capacity of 50 000 ova, plumbed and screened so as to maintain a continuous flow of upwelling water and covered with a close-fitting lid. Survival to hatch usually ranges from 95 to 99%. After hatching, fry were trough-reared to a mean weight of 0.5 g and then

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transferred to the main raceways. Fish were fed a commercially produced dry pellet diet, similar to that described by Hardy (1989).

The hatchery originally was developed primarily as a government-funded research facility (Unwin et al. 1989), with supplementation of the Glenariffe Stream spawning run an important secondary objective. However, as the number and scale of commercial farms increased during the 1980s, the hatchery became the primary source of supply for farmers wishing to obtain stock. During the late 1980s the supplementation role became dominant, so as to allow the demand for farm stock to be met without imposing on the naturally spawning component of the run. Total annual egg take peaked at 12.1 million in 1987 but has since stabilised at 2–3 million, with an average of 460 000 fish being released into the Rakaia River via Glenariffe Stream. The original (i.e., ca. 1978) strategy was to release "90-day" fry at weights of 5–10 g and a similar time of year (November–December) to natural migrants from Glenariffe Stream and the Rakaia River (Unwin 1986; Hopkins and Unwin 1987). This practice led to uniformly poor returns both at Glenariffe and elsewhere in New Zealand (Unwin et al. 1988) and quickly resulted in a trend towards later releases of larger fish (Unwin 1997). Prior to 1982, most fish were released at ages of 5–7 months, but later releases were generally made at ages of 9–11 months and weights of 40–70 g (Table 1). Although this release strategy is at variance with the migratory behaviour of naturally produced fish (Unwin and Quinn 1993), all successful releases of chinook from New Zealand hatcheries have followed this timetable (Unwin et al. 1988).

Table 1. Releases of hatchery-reared chinook salmon juveniles into Glenariffe Stream, BYs 1977–1990.

BY	Number released	Mean age at release (months.days)	Mean weight at release (g)	% tagged
1978	123 000	6.17	14	100
1979	247 000	7.16	28	49
1980	384 000	5.24	11	28
1981	337 000	5.18	15	29
1982	370 000	9.29	24	100
1983	553 000	10.24	34	100
1984	644 000	9.21	49	24
1985	229 000	11.02	61	35
1986	329 000	11.22	65	11
1987	575 000	10.21	55	6
1988	396 000	9.14	51	15
1989	542 000	9.16	66	12
1990	678 000	7.05	40	16

Methods

The primary source of data for this study was the counting fence on Glenariffe Stream (Flain 1982; Quinn and Unwin 1993). Although some aspects of data collection have varied since 1965, date of capture, sex, and fork length (FL) measured to the nearest millimetre are available for all fish intercepted at the fence. We used median date of entry as a measure of run timing for any given year. Data collected via the trap on the hatchery outfall also provided a complete census (including sex and FL) of all fish entering the hatchery, but subsequent handling procedures obscured the precise timing of the spawning runs. Fish entering the hatchery were guided into a holding pen that was inspected two or three times a week, at which times males and females were separated and sorted according to ripeness. Fish not required for hatchery supply were counted immediately and transferred back to Glenariffe Stream, but the remaining fish were not counted until they were spawned. For females, this was usually within 5–10 days of entry, but males tended to be retained as long as they were still able to produce milt and may have been held for up to a month before being recorded and tallied. Consequently, the true median entry dates for chinook intercepted at the hatchery outfall are considerably earlier (at least 5 days) than indicated by the raw data.

Coded-wire tagging (Jefferts et al. 1963) was used routinely to mark a proportion of the hatchery fry released each year (Table 1), all tagged fish being identified externally by removal of the adipose fin (Unwin et al. 1987, 1988). Snouts from all returning adults marked with coded-wire tags (CWTs) were dissected for tag recovery, so that with the exception of lost tags (typically 5% of the total (Unwin et al. 1987)), CWT recovery records for adult chinook entering Glenariffe Stream are complete.

Age at maturity was determined for a subsample of each year's run using otoliths, scales, and (from 1980) CWT data. From 1967–1982, otoliths were collected from spent carcases recovered above the fence, all fish having been marked during passage through the counting fence with a numbered plastic tag attached to the gill cover that enabled over 90% of the carcases to be matched up with the fence records (Flain 1982). On average, age data were available for 56% of the annual run. Because carcase recoveries were biased in favour of larger (and hence older) fish (Flain 1982; Quinn and Unwin 1993), we used mixture analysis (Macdonald and Pitcher 1979) to estimate the true proportions and mean FL for each age-class. These calculations were carried out using version 3.1a of the software package MIX (Macdonald and Green 1988), based on the complete length frequency distribution from the upstream fence records and the length at age data for the subsample of aged carcases. In practice, 2-year-old males were readily identifiable from the length distribution alone, but length distributions for 3- and 4-year-old fish of both sexes overlapped strongly. Excellent fits to the data were obtained using unconstrained Weibull distributions (which can exhibit negative skewness, e.g., Johnson et al. 1994) for males and normal distributions for females, p-values for goodness-of-fit tests based on the χ^2 distribution averaging 0.35. Mean SEs for the distribution parameters estimated by MIX were ±6 mm for mean FL at age and ±1.5% for the percentages in each age-class.

From 1983 to 1994, age determinations were based on scale analysis (Flain and Glova 1988), supplemented by CWT data. We estimated numbers of natural and hatchery-origin chinook returning each year, and mean FL by sex and age, from CWT recoveries and from scale pattern analysis (SPA) (Unwin and Lucas 1993). Prior to 1987, expanded CWT returns gave consistent and reliable estimates of the hatchery contribution, particularly for the 1978 and 1982–1983 brood years when the tagging fraction was 100%. To estimate the number of naturally produced fish of each sex and age-class for these years, we subtracted the estimated hatchery component from the total run and used MIX to analyse the remaining length frequency and age subsample data. After 1987, this procedure sometimes gave unreliable estimates for the natural run parameters, particularly for brood years when the tagging fraction was low (6–16%; see Table 1) and (or) the natural run was weak. To refine the estimates for these years, we used SPA to identify natural and hatchery fish for the same subsample of fish used for age determination, and hence to estimate mean FL ± 1 SD for each combination of age-class, sex, and origin. We then used MIX to estimate numbers of natural and hatchery fish in each age-class, using the SPA and CWT estimates of mean FL at age, and expanded CWT estimates of the number of hatchery fish, to constrain the initial fitting procedure. Finally, we incrementally relaxed as many constraints as possible while still obtaining a satisfactory fit to the raw data. Mean SEs for the 1987–1994 parameter

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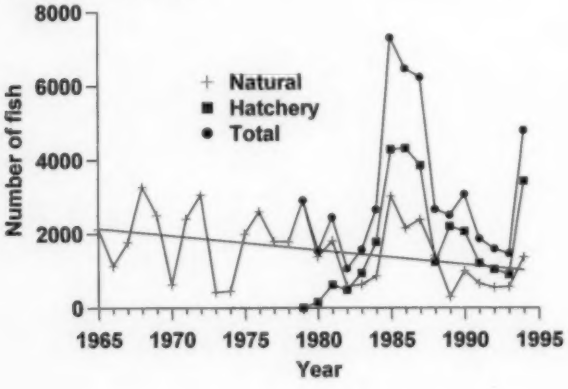
Fig. 1. Chinook salmon spawning runs in Glenariffe Stream, 1965–1994. The straight line is the linear regression of the number of naturally produced spawners (S_N) on year (Y), given by $S_N = 2136 - 38.4 \times (Y - 1965)$.



estimates were ±11 mm for mean FL at age and ±2.2% for the percentages in each age-class.

Throughout this paper, we use the term "brood year" (BY) to refer to the cohort descended from one year's spawning and returning as adults over the next 2–5 years and the term "spawning year" (SY) to refer collectively to all the returns in a single season, comprising adults from up to four successive BYs. We follow North American usage and refer to males returning at the end of their second year as jacks. This term is not used in New Zealand, where jacks (and the occasional 2-year-old female) are regarded as an integral part of adult spawning runs (Quinn and Unwin 1993).

Results

Run strength

From 1965 to 1979, before returns of hatchery fish began, annual chinook salmon spawning runs in Glenariffe Stream averaged 1917 fish and ranged from 424 to 3264 (Fig. 1; Table 2). Since 1980, both the minimum and maximum annual spawning runs have more than doubled (to 1058 and 7288 fish, respectively), but there has been no consistent increase in total run strength over the 30 years from 1965 to 1994. The correlation between total run strength and year is positive but not significant ($r^2 = 0.122, p = 0.063$) and is strongly influenced by the most recent (1994) datum. Excluding this point from the regression calculation considerably weakens the observed correlation ($r^2 = 0.086, p = 0.122$). The natural component of the run has decreased since 1980 (1980–1994 average 1165 fish) and shows a slight negative correlation with time from 1965 to 1994 ($r^2 = 0.138$, $p = 0.045$). Over the last 5 years (1990–1994), natural fish constituted 34% of the population (range 29–39%).

For adult chinook of natural origin, we determined the proportion of ocean- and stream-type adults for SY 1989–1992 using data from Unwin and Lucas (1993) and combined these data with estimates for SY 1993–1994 based on SPA. Stream-type fish constituted 14.2% (range 6.1–24.4%) of the natural population for these six years. Comparable data for Glenariffe Stream prior to 1980 are not available, but between 1967 and 1976, stream-type adults made up 37.8% (range 21.2–45.6%) of Rakaia River chinook (Quinn and Unwin 1993). The decline in run strength for natural chinook in Glenariffe Stream therefore appears to have been most pronounced among stream-type fish.

The natural and hatchery components of the spawning run showed a clear tendency to home on the counting fence and the hatchery outfall, respectively. For SY 1990–1994, we estimated the incidence of natural and hatchery-origin fish entering via the two traps from SPA and CWT recovery data. Fish of natural origin accounted for 52–69% of the fish intercepted at the fence, compared with 19–31% recorded at the hatchery outfall (Table 3). However, less than one quarter of the returning fish (5–23%) were caught at the counting fence, and a breakdown of the totals for each trap by origin shows that over half of the naturally produced fish (54–87%) entered the hatchery trap.

Age at maturity

For male chinook, age at maturity (as measured by the mean age of spawning fish) decreased from SY 1967 to SY 1994. Mean age for all spawning males (combining fish of natural and hatchery origin from SY 1980 onwards) showed a weak negative correlation with time ($r^2 = 0.133$, $p = 0.056$). This decrease was attributable partly to a tendency for hatchery males to mature earlier than those of natural origin, but also reflected a decline ($r^2 = 0.171$, $p = 0.029$) in the mean age of naturally produced males (Fig. 2). Mean age at maturity for males of natural and hatchery origin did not differ for the 13 cohorts from BYs 1978–1990 (hatchery = 2.69 years, natural = 2.73 years; $t = 0.44$, $p = 0.66$). However, natural males from BYs 1965–1977 (mean age 2.87 years), which predated the first hatchery releases (BY 1978), were older than hatchery males from the post-1978 cohorts ($t = 2.69$, $p = 0.015$).

To investigate the age of male spawners in more detail, and in particular to assess whether the decline in the age of naturally produced males may have been related to the increasing presence of hatchery fish, we examined return data for fish of natural and hatchery origin in terms of the proportion of jacks. Preliminary analysis of these data suggested that despite the absence of any difference in mean age between natural and hatchery males from BYs 1978–1990, the age structure of hatchery males tended to be more variable between years than for naturally produced males, with a higher incidence of jacks. Among males of natural origin (SY 1967–1994; 28 years), jacks constituted 7–59% of the total (average 28%) and exceeded 50% only once (in 1986). For males of hatchery origin (SY 1982–1994; 13 years), jacks constituted 4–80% of the spawning run (average 39%) and exceeded 50% on four occasions.

To quantify fluctuations in jack abundance among naturally produced chinook, we determined the age structure for male and female chinook spawning in Glenariffe Stream each SY by combining records for fish entering via the counting fence with records for hatchery fish, surplus to ova requirements, that were transferred to Glenariffe Stream above the counting fence and allowed to spawn naturally. We then compared these results with the age structure for subsequent returns from each cohort. For male chinook, age of parent stock was positively correlated with the age at return, in terms of both mean age at maturity ($r^2 = 0.315$, $p = 0.003$, $n = 26$) and the percentage incidence of jacks ($r^2 = 0.507, p < 0.001$; Fig. 3). Although this relationship was not strongly apparent when jack spawners

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Table 2. Chinook salmon spawning runs into Glenariffe Stream, 1965–1994, by origin and age.

	Age at maturity								
	Natural origin				Hatchery origin				% of natural origin
Year	2	3	4	Total	2	3	4	Total	
1965	143	1487	488	2119	0	0	0	0	100
1966	135	587	412	1134	0	0	0	0	100
1967	400	1238	127	1769	0	0	0	0	100
1968	145	2857	262	3264	0	0	0	0	100
1969	92	976	1417	2489	0	0	0	0	100
1970	109	305	213	629	0	0	0	0	100
1971	351	1938	107	2396	0	0	0	0	100
1972	173	2274	595	3043	0	0	0	0	100
1973	62	231	131	424	0	0	0	0	100
1974	144	234	70	452	0	0	0	0	100
1975	558	1397	34	1989	0	0	0	0	100
1976	160	2237	190	2587	0	0	0	0	100
1977	351	1026	412	1789	0	0	0	0	100
1978	270	1457	56	1783	0	0	0	0	100
1979	232	2418	237	2887	4	0	0	4	100
1980	289	838	255	1382	111	40	0	151	90
1981	86	1452	270	1808	125	493	4	622	74
1982	103	425	46	575	82	351	50	483	54
1983	196	400	35	631	470	390	75	935	40
1984	221	593	45	859	643	1076	60	1779	33
1985	340	2361	308	3009	1001	3015	263	4279	41
1986	750	1161	233	2144	988	2704	617	4309	33
1987	165	1945	265	2375	281	2483	1085	3850	38
1988	288	779	342	1409	325	383	524	1236	53
1989	100	188	10	298	1243	939	8	2194	12
1990	72	898	29	999	113	1915	30	2058	33
1991	157	425	70	652	129	683	397	1209	35
1992	73	450	29	552	14	795	231	1040	35
1993	161	399	8	568	277	551	72	900	39
1994	75	1261	33	1369	152	3066	203	3420	29

Note: Five-year-old fish (0.04% of the population) are not tabulated separately, but are included in the totals.

constituted less than about 40% of the spawning population, higher proportions of jack spawners (>50%) were always associated with high returns of jacks. In particular, jack returns from BY 1986 (for which jacks constituted 74% of the male spawners) accounted for 72% of the returning males. With one exception (BY 1970), all BYs for which jacks made up at least 35% of returning males occurred after hatchery releases began in 1978. This relationship produced a strong negative correlation ($r^2 = 0.516$, $p < 0.001$) between age at maturity for male chinook and the proportion of jack spawners.

None of the age-related trends that we observed for male chinook applied to females. Age at maturity for female chinook of natural origin was uncorrelated with time ($r^2 = 0.020$, $p = 0.486$) and averaged 3.16 years (Fig. 2). Mean age at maturity did not differ between females of natural and hatchery origin ($t = 0.45$, $p = 0.65$), and there was no correlation between mean age at spawning and mean age at return ($r^2 = 0.001$, $p = 0.90$).

Length at age

Among male chinook, fish of hatchery origin were smaller than those of natural origin (nested ANOVA, origin × age, $F_{1,117} = 21.2, p < 0.001$). Mean FL for hatchery fish (calculated as the mean of the annual mean FL for each age-class) was consistently smaller than for naturally produced fish maturing at ages 2–4 (Table 4), although the difference tended to decrease with increasing age. For 2-year-olds the discrepancy (59 mm) was highly significant and amounted to an 11% decrease in FL for fish of hatchery origin. However, there was no evidence of any similar trend among female spawners (nested ANOVA, origin × age, $F_{1,110} = 0.092$, $p = 0.76$). Three-year-old females of hatchery origin (mean FL = 727 ± 8 mm) were smaller than those of natural origin (mean FL = 746 ± 5 mm), but the difference was barely significant ($t = 2.02$, $p = 0.05$) and was not apparent for either 2-or 4-year-old fish (Table 4).

Mean FL of naturally produced chinook was uncorrelated with time for both males and females and for all age-classes ($p > 0.3$ in all cases). However, the increasing numbers of hatchery-origin fish in spawning runs after 1980, and the high incidence of jacks and smaller size at age among 2-and 3-year-old males of hatchery origin, combined to generate a pronounced decline in mean FL of spawning males from 1967 to 1993 (Fig. 4). Mean FL was negatively correlated with time over this period ($r^2 = 0.215, p = 0.013$), linear regression of FL on year yielding a coefficient of –3.1 mm/year, equivalent to

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Table 3. Chinook salmon spawning runs in Glenariffe Stream, 1990–1994, by origin of fish (natural or hatchery) and interception point (the counting fence on Glenariffe Stream or the hatchery outfall).

Year	Interception point	Origin of fish		Total	Fish of natural origin as % of total
		Natural	Hatchery		
1990	Counting fence	326	300	626	52
	Hatchery	583	1848	2431	24
	Total	909	2148	3057	30
	Fence catch as % of total	36	14	20	
1991	Counting fence	55	43	98	56
	Hatchery	370	1393	1763	21
	Total	425	1436	1861	23
	Fence catch as % of total	13	3	5	
1992	Counting fence	146	66	212	69
	Hatchery	428	952	1380	31
	Total	574	1018	1592	36
	Fence catch as % of total	25	6	13	
1993	Counting fence	251	113	364	69
	Hatchery	301	902	1202	25
	Total	552	1014	1566	35
	Fence catch as % of total	46	11	23	
1994	Counting fence	651	370	1021	64
	Hatchery	717	3051	3768	19
	Total	1368	3421	4789	29
	Fence catch as % of total	48	11	21	

Fig. 2. Mean age at maturity for male and female chinook salmon spawning in Glenariffe Stream, 1967–1994. The straight line is the linear regression of mean age for male spawners (A_m) on year (Y), given by $A_m = 2.8 - 0.0111 \times (Y - 1967)$.

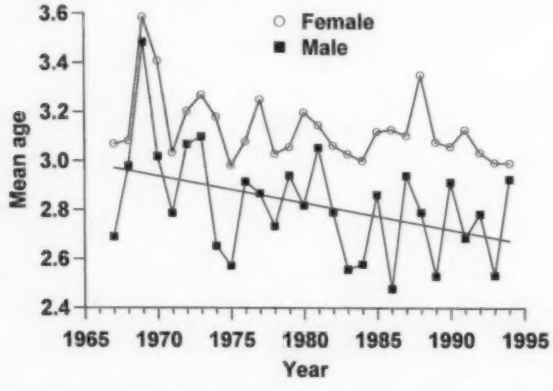
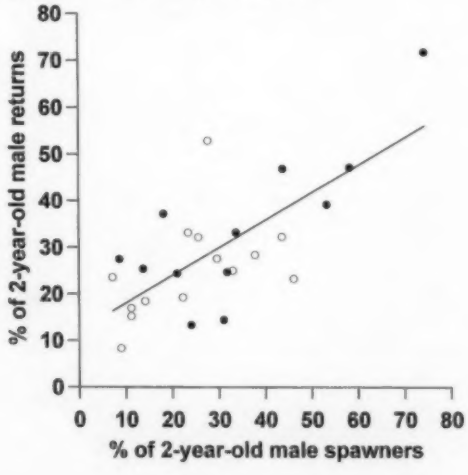


Fig. 3. Percentage incidence of 2-year-old male (jack) spawners versus percentage incidence of jack returns in Glenariffe Stream, BYs 1967–1990. BYs 1979–1990, which included spawning fish of hatchery origin, are denoted by solid symbols.



an 86-mm decrease in mean FL over a 28-year period. Mean FL for the period 1967–1980 (727 mm) was 55 mm greater than for the period 1981–1994 (672 mm). The most extreme reduction in mean FL occurred in SY 1989, when a strong return of hatchery-origin jacks from BY 1987 coincided with weak returns of naturally produced 3- and 4-year-old fish from BYs 1986 and 1985, respectively, to yield a mean FL of 558 mm.

Run timing

Median stripping dates for supply of ova to the hatchery have become progressively earlier since 1978 (Fig. 5), largely in response to a demand from commercial salmon farmers for maximum fry size as early as possible. To assess whether this practice had selected for earlier spawning dates in subsequent runs, we examined median dates of entry for fish intercepted at the counting fence from 1965 to 1994 for evidence of long-term trends. Based on regression analysis of median entry date on year, there was no evidence of any consistent linear trend over the period of record, for either females ($r^2 = 0.053$, $p = 0.22$) or males ($r^2 = 0.001$, $p = 0.86$). However, there was some evidence that run timing has become more variable (Fig. 6).

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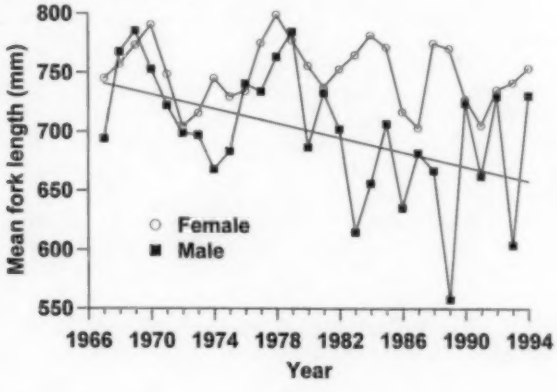
Table 4. Mean FL ± 1 SE by sex and age for chinook salmon spawning in Glenariffe Stream, 1967–1994 (natural origin) and 1979–1994 (hatchery origin).

	Age at maturity	FL ± 1 SE (mm)		Significance level, p
		Natural	Hatchery	
Males	2	560±8	501±5	<0.001 (40)
	3	768±9	740±7	0.017 (39)
	4	843±18	824±10	0.302 (38)
Females	2	589±26	604±6	0.416 (33)
	3	746±8	727±5	0.050 (39)
	4	813±11	809±8	0.808 (38)

Fig. 4. Mean FL for male and female chinook salmon spawning in Glenariffe Stream, 1967–1994. The straight line is the linear regression of mean FL for male spawners (FL_m) on year (Y), given by $FL_m = 740 - 3.07 \times (Y - 1967)$.



For female chinook, median entry dates over the last 8 years (1987–1994) include five of the six earliest dates recorded (on or before 26 April) and three of the four latest dates (on or after 6 May). Similarly, median entry dates for male chinook over the same period include four of the five earliest dates (on or before 22 April) and three of the four latest dates (on or after 2 May). Standard deviations for median entry dates pre-1981 (females 4.3 days; males 3.2 days) were, respectively, 1.6 and 2.6 times less than those recorded post-1981 (females 6.8 days; males 8.2 days). Median entry dates for chinook intercepted at the hatchery from 1987 to 1994 were 27 April for females and 24 April for males, 2–4 days earlier than for naturally produced chinook over the period 1965–1981 (Quinn and Unwin 1993).

Discussion

On the basis of this study, we reject the hypotheses that there have been no changes in life history parameters for Glenariffe Stream chinook salmon since 1965. Despite considerable interannual variation, our results show significant long-term trends in several life history traits, all of which can be linked wholly or partly with the increasing presence of hatchery fish since ca. 1980. The strongest changes we detected were the decline in mean age at maturity and mean FL in male spawners. Jacks made up a higher proportion of the returns in years

Fig. 5. Median spawning date for female chinook salmon used for ova supply to Glenariffe Hatchery, 1979–1994.

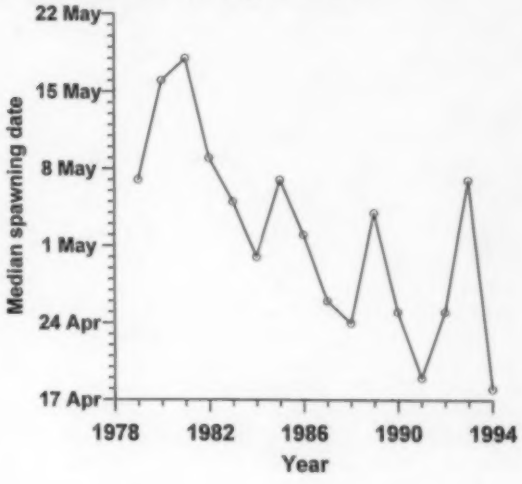
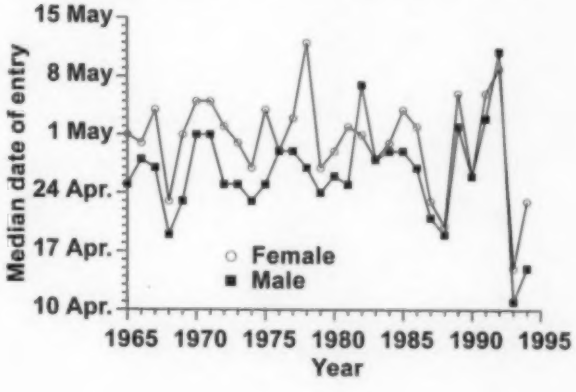


Fig. 6. Median spawning date for male and female chinook salmon entering Glenariffe Stream via the counting fence, 1965–1994.



when hatchery fish were present, with the mean age of naturally produced male spawners decreasing from 2.87 years for BYs 1965–1977 to 2.60 years for BYs 1978–1990. Mean FL for all male spawners returning between 1981 and 1994 was 55 mm less than for those returning prior to 1980, due to the increase in jack returns and a smaller FL at age for hatchery fish. For chinook of natural origin, there was also evidence of a decline in run strength, particularly in stream-type fish, and a tendency towards increased variability in spawning dates.

For changes of this magnitude to develop and be sustained as a result of hatchery releases, in what was originally a naturally sustained population, three processes need to occur. Firstly, adults of hatchery origin must differ from naturally produced adults in one or more life history traits. Whether this difference is related to environmental effects such as hatchery feeding and (or) growth regimes (e.g., Bilton et al. 1982; Brannon et al. 1982) or to hatchery procedures that select for traits such as early maturation (e.g., Siitonen and Gall 1989; Hansen and Jonsson 1991) is immaterial. Secondly, hatchery fish must

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have higher survival than natural fish, so that hatchery fish can eventually come to dominate the population (Helle 1981). Thirdly, hatchery fish must be able to spawn successfully in the wild, so that interbreeding (and possibly gene flow) between the hatchery and natural populations can take place (Hindar et al. 1991; Waples 1991). All of these conditions appear to apply in Glenariffe Stream.

The most striking feature of recent Glenariffe Stream spawning runs is the extent to which the naturally spawning population that existed up to ca. 1980 and the more recent hatchery-reared component have now merged into what is effectively a single population. Hatchery fish have outnumbered naturally produced fish every SY since 1983, constituting 59–88% of the population (see also Unwin and Lucas 1993). Up to 1985, 24–100% of hatchery fish were coded-wire tagged (and hence externally identifiable by the absence of the adipose fin), so that hatchery fish could often be separated from those of natural origin. For BYs 1986–1991, however, the tagging fraction ranged from 16% to a minimum of 6% in 1987, so that most hatchery fish were unmarked and could be distinguished (retrospectively) only by scale analysis (Unwin and Lucas 1993). Although the trap on the hatchery outfall was successful in capturing 86–97% of the returning hatchery fish, 31–48% of the fish entering Glenariffe Stream via the counting fence from 1990 to 1994 were of hatchery origin. Several authors have noted that, provided returns of hatchery fish can be handled separately from preexisting wild or naturally maintained stocks, the integrity of these stocks will remain intact (Helle 1981; Hindar et al. 1991; Waples 1991). Despite the establishment of independent trapping facilities on the main stream and the hatchery outfall, this separation has not been achieved in Glenariffe Stream. This may be due to the close proximity of the two traps (cf. Unwin and Quinn 1993) and the fact that the hatchery is supplied with water from the same spring-fed system as Glenariffe Stream.

The small size of hatchery chinook compared with those of natural origin, in 2-year-old and to a lesser extent 3-year-old males, is consistent with differences in mean size between yearlings of natural and hatchery origin. While they are reared under a hatchery feeding regime, chinook fry grow more rapidly than their counterparts in Glenariffe Stream and the Rakaia River (Unwin and Lucas 1993). However, because hatchery rearing typically continues until autumn or winter, naturally spawned fry that migrate from the lower Rakaia River in late spring and early summer (Hopkins and Unwin 1987) spend several months feeding at sea before hatchery fry are released. During this period, their rapid growth more than compensates for their slower growth rate in freshwater, so that at 1 year of age, they are substantially larger (mean FL 231 mm) than hatchery fish (mean FL 169 mm; Unwin and Lucas 1993). Since hatchery fish maturing in their second year of life have little more than 6 months of marine growth (August–January) before they reenter freshwater, the discrepancy in size between natural and hatchery fish is most pronounced among 2-year-old fish. It is unclear why females do not show a similar effect, although 2-year-old females are rare (Quinn and Unwin 1993) and our estimates of their mean FL are correspondingly poor.

The increased incidence of jacks in returns of hatchery chinook to Glenariffe Stream is consistent with the general trend towards early maturation in hatchery salmonids. It is well established that age at maturity is negatively correlated with growth rate and that increased growth rates typically attained in hatchery environments are associated with early (or precocious) maturation, particularly in males (e.g., Bilton et al. 1982; Brannon et al. 1982; Thorpe 1986 and references therein). While the physiological processes which trigger the onset of sexual maturity are not fully understood, there is evidence that maturation is associated with age- and sex-specific minimum threshold sizes (Thorpe 1986; Hankin et al. 1993). In male Atlantic salmon (*Salmo salar*), precocious (age 2) maturation appears to be related to springtime fat reserves during the second year of life (Rowe and Thorpe 1990). The tendency for hatchery releases to produce jacks therefore appears to be at least partly driven by hatchery rearing practices.

Notwithstanding the above mechanism, which is environmentally rather than genetically controlled, changes in the age structure of naturally spawned chinook also appear to reflect genetic influences. The positive correlation between the incidence of jacks in the spawning and returning populations suggests a heritable tendency for males to mature at age 2, which is linked to the abundance of 2-year-old males in the parent stock. However, although age at maturity in salmonids is subject to genetic control (e.g., Ricker 1972; Brannon et al. 1982; Gjerde 1984; Hankin et al. 1993), spawners that have matured at age 2 because of rapid growth within the hatchery have not necessarily been genetically selected for early maturation. For naturally produced males to inherit a tendency to mature at age 2 in BYs when a high proportion of the parent stock comprises jacks, there must be some other process associated with hatchery releases at Glenariffe that tends to select for younger-maturing fish.

We suggest that this process arises because of differential selection, induced by extended hatchery rearing for 8–12 months, of ocean- and stream-type fry. Within their native North American range, these two life history types are phenotypically and genetically distinct (Carl and Healey 1984; Clarke et al. 1992, 1994) and are usually associated with fall- and spring-run chinook salmon stocks, respectively. New Zealand stocks are unusual among fall-run chinook in that both life history types are common, adults with a stream-type life history accounting for just over one third (38%) of the adult stocks in the Rakaia River prior to 1980 (Quinn and Unwin 1993). The two phenotypes differ with respect to date of entry to the river mouth, length at age, and also age at maturity, with ocean-type fish tending to mature 1 year earlier (at ages 2 and 3) than stream-type fish, which mature at ages 3 and 4 (Quinn and Unwin 1993). However, both types spawn concurrently within Glenariffe Stream, and there is no evidence of any mechanism that would prevent interbreeding. We therefore assume that each adult pair has the potential to contribute both ocean- and stream-type individuals to the ensuing cohort, although their relative abundance may well vary between families. For annual cohorts from Glenariffe Stream prior to 1980, ocean-type fry presumably outnumbered stream-type fry by substantially more than 2:1 at the time of hatching, but were subject to significantly higher mortality rates as the cohort aged because of their smaller size at ocean entry (Unwin and Lucas 1993). Hatchery rearing for 8–12 months would therefore greatly increase the survival potential of ocean-type fry, but would be less beneficial to stream-type fry. By differentially affecting survival rates in this way, hatchery releases

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would thus tend to select for ocean-type fish, and hence (because ocean-type fish are more likely to mature at age 2 than stream-type fish) for 2-year-old fish. This hypothesis is also consistent with the decrease in returns of stream-type adults that we observed in Glenariffe Stream.

Run timing varies widely between salmon populations (Brannon 1987; Quinn and Unwin 1993), and is highly heritable (e.g., Ricker 1972), with changes of over 6 days per generation (over six generations) recorded for rainbow trout subject to an artificial selection regime (Siitonen and Gall 1989). Given the trend towards earlier spawning dates for hatchery stock, we might expect that date of entry to Glenariffe Stream for hatchery-origin chinook should become progressively earlier. Our results are confounded by delays in recording entry date for individual fish intercepted at the hatchery and do not unequivocally demonstrate any such trend. However, with true entry dates likely to be at least 5 days earlier than the raw data indicate, the 2- to 4-day advance in spawning date shown by our results is consistent with an advance of at least 1 week, and perhaps as much as 2 weeks, over a period of 10–15 years or three to four generations.

Changes in Glenariffe Stream chinook since the introduction of hatchery fish therefore appear to reflect a combination of environmental and genetic factors. The smaller size at age and increased incidence of jacks in hatchery males can be readily accounted for in terms of environmental processes (via hatchery rearing practices). By contrast, the variations in run timing, increased incidence of jacks, and declining incidence of stream-type adults recorded at the counting fence appear to have both an environmental and a genetic component. Any loss of genetic diversity has potentially significant evolutionary implications, since any genes lost to the population are most unlikely to reemerge spontaneously over a similar time scale. However, changes arising from environmental effects associated with hatchery operations could probably be reversed within a few generations, and the status quo of the late 1970s regained, through appropriate management strategies (e.g., Helle 1981; Hindar et al. 1991; Waples 1991). In the Pacific Northwest, where salmon display extensive genetic variation throughout their natural range, and hatchery releases have continued for over a century, reversal of any hatchery-induced changes may be more difficult to achieve. While the details of the Glenariffe programme are unusual by North American standards, and may have no direct counterpart among U.S. and Canadian chinook hatcheries, operations at Glenariffe have clearly had unforeseen and potentially undesirable consequences. In particular, the hope that hatchery supplementation of Glenariffe Stream would generate a surplus for farm supply without impacting on the natural population has not been realised.

Our conclusions regarding the influence of hatchery releases on the relative abundance of ocean-and stream-type fish may shed some light on the process by which chinook have adapted to New Zealand conditions. Many North American rivers, including the Sacramento as it was in the 1900s, are characterised by extensive estuaries that provide an abundance of intertidal rearing habitat for juvenile chinook (Healey 1982). In contrast, New Zealand east coast rivers have virtually no estuarine reaches (e.g., Eldon and Greager 1983) and discharge directly into the ocean. Among present-day Sacramento River fall chinook, ocean-type fry apparently migrate downriver relatively quickly, after which they typically spend 2 months rearing in the estuary where they grow to about 70 mm FL (Kjelson et al. 1982). Given the degree of water withdrawal from the Sacramento River over the last century, ocean-type fry in the 1900s may have been even more strongly adapted to a gradual ocean entry than present-day stocks. However, while this adaptation is well suited to rivers such as the Sacramento, the lack of estuaries in local rivers such as the Rakaia and Waitaki suggests that ocean-type behaviour may be less appropriate for New Zealand rivers. If so, selection would tend to favour juveniles that spent a longer period in freshwater before entering the ocean and might eventually lead to stream-type behaviour emerging in what was originally an ocean-type stock. The mixture of ocean- and stream-type life histories in New Zealand chinook may therefore be a direct response to local environmental conditions, in an evolutionary process that is still continuing. The most significant impact of hatchery releases on New Zealand chinook may therefore be that, by favouring the development of ocean-type fish, their adaptation to New Zealand rivers has been temporarily reversed.

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Fry-to-adult survival of natural and hatchery-produced chinook salmon (*Oncorhynchus tshawytscha*) from a common origin

M.J. Unwin

Abstract: Fry-to-adult survival rates for chinook salmon (*Oncorhynchus tshawytscha*) from Glenariffe Stream, a tributary of the Rakaia River, New Zealand, were estimated for fish of both natural and hatchery origin. Survival of naturally produced fry, most of which leave Glenariffe Stream within 24 h of emergence, averaged 0.079% (range 0.013–1.17%). For hatchery fish released at 8–12 months, standardised to a mean weight of 38 g, survival covaried with weight at release consistently across all brood years and averaged 0.34% (range 0.008–3.28%). Survival rates for hatchery fish were four times higher than for naturally produced fry, but were extremely poor relative to their size at release. Survival rates for fish of natural and hatchery origin were positively correlated, suggesting that recruitment of both stocks is primarily controlled by common influences within the marine environment, probably during the first winter at sea. Stock–recruitment analysis for the natural population showed little tendency for recruitment to increase with stock size, suggesting that marine survival rates may be density dependent. Although the reasons for the relatively poor survival of hatchery fish are unclear, the results provide a case study in which hatchery fish appear to have a poorer "fitness to survive" than their natural counterparts.

Résumé : Les taux de survie d'alevin à adulte du saumon chinook (*Oncorhynchus tshawytscha*) du ruisseau Glenariffe, tributaire de la rivière Rakaia, en Nouvelle-Zélande, ont été estimés pour les poissons d'origine naturelle et les poissons d'élevage. La survie des alevins produits naturellement, dont la plupart quittent le ruisseau Glenariffe en l'espace de 24 h après l'éclosion était en moyenne de 0,079 % (étendue : 0,013 à 1,17 %). Dans le cas des poissons d'élevage libérés à 8–12 mois, standardisés à un poids moyen de 38 g, la survie a covarié avec le poids à la libération de manière constante au cours de toutes les années de génération, et était en moyenne de 0,34 % (étendue : 0,008 à 3,28 %). Les taux de survie des poissons d'élevage étaient quatre fois plus élevés que ceux des alevins naturels, mais étaient extrêmement médiocres par rapport à leur poids à la libération. Les taux de survie des poissons naturels et d'élevage étaient corrélés positivement, ce qui indiquerait que le recrutement des deux stocks est régulé principalement par des influences communes dans l'environnement marin, probablement au cours du premier hiver en mer. L'analyse stock–recrutement de la population naturelle a montré que le recrutement avait peu tendance à augmenter avec la taille du stock, ce qui pourrait signifier que les taux de survie en mer pourraient être dépendants de la densité. Bien que les raisons expliquant la survie relativement médiocre des poissons d'élevage soient obscures, les résultats obtenus fournissent un cas-type où les poissons d'élevage semblent moins adaptés pour survivre que leurs congénères d'origine naturelle.
[Traduit par la Rédaction]

Introduction

Throughout the Pacific northwestern United States and Canada, concerns about declining stocks of anadromous salmonids have prompted increasing speculation about the long-term viability of some Pacific salmon (*Oncorhynchus* spp.) stocks. Despite ongoing and long-standing attempts to restore potentially threatened stocks through releases of hatchery-reared fish, a 1991 study identified 214 stocks of salmon, steelhead trout (*Oncorhynchus mykiss*), and cutthroat trout (*Oncorhynchus clarki*) as significantly depleted, including 101 considered to be at high risk of extinction (Nehlsen et al. 1991). Although factors such as overfishing, habitat modification, and hydroelectric development have long been recognised as contributing to this decline (Stickney 1994), a more recent concern is that, albeit inadvertently, hatchery releases have also been a contributing factor (Hindar et al. 1991; Hilborn 1992).

Numerous studies have demonstrated behavioural and genetic differences between salmonids of wild and hatchery origin (see Hindar et al. (1991) for a review), and the potential for detrimental impacts on the genetic integrity of wild stocks is well recognised (e.g., Waples 1991; Waples and Do 1994). Another concern is the possibility of adverse impacts on wild stocks through increased competition for food and (or) habitat in the ocean (Cooney 1993; Hilborn and Winton 1993). However, few if any studies provide unequivocal evidence that these potential impacts have actually materialised, to the detriment of wild stocks (Daley 1993). A recent critique of the Canadian Salmonid Enhancement Programme (SEP) points out that a full assessment of SEP's contribution to harvest levels, taking into account the contribution from both wild and

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hatchery stocks, is virtually impossible because of a lack of quantitative data on spawning success, productivity, and adult survival rates for natural stocks (Winton and Hilborn 1994). For example, Reisenbichler and McIntyre (1977) reported that egg-to-fry survival for hatchery steelhead trout was lower than for fry of wild origin, but their study did not extend to assessing differences in survival to maturity. The present study compares survival to maturity for fall-run chinook salmon (*Oncorhynchus tshawytscha*) of natural and hatchery origin in a New Zealand stream.

Since 1978, chinook salmon spawning runs in Glenariffe Stream (a tributary of the Rakaia River) have been supplemented by hatchery releases, to the extent that naturally spawning stocks now comprise an undifferentiated mix of natural- and hatchery-origin fish (Unwin and Glova 1997). Nevertheless, with respect to the Rakaia River and the oceanic phase of the life cycle, juvenile production from Glenariffe Stream can still be grouped into two distinct categories. One group, consisting of fry emerging from naturally constructed redds, represents the progeny of all naturally spawning fish, irrespective of whether one or both parents were of natural or hatchery origin. The second group consists of juveniles reared at the Glenariffe Hatchery, typically for 6–12 months, and released into the Rakaia River at weights of up to 100 g.

A key finding of an intensive downstream trapping programme on Glenariffe Stream from 1973 to 1976 was that egg-to-fry survival is relatively constant from year to year (average 47.6%; range 37.9–52.1%) and is uncorrelated with spawning stock size despite a 10-fold variation in annual ova deposition (Unwin 1986). In this paper, I exploit this consistency to achieve three primary objectives. Firstly, I analyse the naturally spawning chinook population in Glenariffe Stream, over the period 1965–1990, considering annual variability in fry-to-adult survival and the relationship between stock size (as measured by fry production) and subsequent adult recruitment (as measured by returns at maturity). Secondly, I analyse returns of hatchery fish from the 1978–1990 brood years (BYs), in terms of annual variability in survival and the relationship between survival and weight at release. Thirdly, I compare survival rates for chinook of natural and hatchery origin, over the period spanning entry to the upper Rakaia River, downriver migration, seawater entry, and subsequent growth to maturity. A preliminary objective, addressed in the next section of this paper, was to estimate egg-to-fry survival for natural-origin chinook from BY 1992, and hence to assess whether egg-to-fry survival had changed since the 1973–1976 study.

Methods

Adult spawning runs

Glenariffe Stream is a stable, spring-fed tributary of the Rakaia River and supports a mean annual spawning population of 1920 chinook salmon (see Unwin (1986) and Unwin and Glova (1997) for more detailed descriptions). Spawning runs have been monitored annually since 1965 via daily counts at an upstream counting fence (Flain 1982; Quinn and Unwin 1993). Since 1978, an average of 460 000 hatchery fish have been released from Glenariffe annually, including an average of 147 000 marked with coded-wire tags (CWTs), as part of a hatchery supplementation programme (Unwin and Glova 1997). Mature adults of both natural and hatchery origin are intercepted at the fence, and all fish not required for hatchery supply or CWT recovery are released above the fence where they are allowed to spawn naturally.

Fish were aged from otoliths and (or) scales collected from a subsample of the fish intercepted at the counting fence (Flain 1982; Flain and Glova 1988), supplemented by CWT recovery data (for fish of hatchery origin). Together with estimates of the relative proportion of natural- and hatchery-origin fish derived from scale pattern analysis (SPA) (Unwin and Lucas 1993), these data provided a complete enumeration of the naturally produced and hatchery contributions to each spawning run by age and (or) BY (see Unwin and Glova (1997) for further details).

Estimation of survival rates

To provide the most direct comparison between survival rates for fish of natural and hatchery origin, I estimated outmigrant-to-adult survival rates for both populations. For hatchery fish, these estimates were derived from CWT recoveries for adults recovered in Glenariffe Stream, calculated for each group of tagged juveniles released from the Glenariffe hatchery. A total of 209 tag groups were released from 1978 to 1990, ranging from 5 in 1978 and 1980–1981 to 62 in 1983, with an average of 9310 tagged juveniles and 50 adult recoveries per release group. I did not adjust the data to take account of adult salmon caught via the sports fishery, which accounts for about one third of the fish entering the Rakaia River (Unwin and Davis 1983; NIWA, unpublished data), or from other sources external to Glenariffe Stream, so that estimates of survival are conservative. For the purposes of this study, ignoring the sports catch is equivalent to the assumption that the variation in catch rate between seasons and (or) between fish of natural and hatchery origin is small compared with interannual variation in marine survival.

To estimate the number of naturally produced fry emigrating from Glenariffe Stream each year, I first estimated the total number of ova deposited by assuming that all females that passed through the counting fence spawned successfully. I then applied the fecundity–length relationship given by Quinn and Bloomberg (1992) (log(fecundity) = 1.81 log(fork length) – 3.50) to estimate fecundity for each spawner, and hence for the total spawning population. My estimates for 1973–1976 therefore differ slightly from those given by Unwin (1986), which were based on an assumed fecundity of 4500 ova per female.

To ascertain whether egg-to-fry survival had changed significantly from the 1973–1976 average, I estimated fry migration for the 1992 spawning season (for which hatchery fish comprised 73% of the fish entering Glenariffe Stream (Unwin and Lucas 1993)) by operating the downstream trap on Glenariffe Stream during spring and summer 1992–1993. Trapping and estimation procedures were identical to those used in the 1973–1976 study. The trap, comprising nine identical inclined plane traps evenly spaced across a weir spanning the full width of the stream, was operated nightly using five of the nine inclined plane traps to intercept approximately one fourth of the stream flow. Trapping continued from 7 August 1992 to 31 January 1993, during which period over 99% of the fry produced in Glenariffe Stream move downstream to the Rakaia River (Unwin 1986). The trap was cleared every morning, all fry being hand counted. Every three nights from 14 August to 15 January, I estimated trapping efficiency by releasing marked fry (which were held over from the previous day's catch and immersed in a 1 : 40 000 solution of Neutral Red for 2 h) into Glenariffe Stream 200 m above the trap site and recording the number of recaptures (R). The average number of marked fry per release (M) was 278. Regression of M on R yielded the relationship $M = 46 + 5.23R$ ($r^2 = 0.858$, $n = 51$), representing a mean trapping efficiency of 19%. I then used this relationship to estimate the total number of fry migrating each night, assuming that the same relation applied to both marked and unmarked fry throughout the trapping period.

Estimated ova deposition and total fry migration for BY 1992 were 489 000 and 243 000, respectively, corresponding to an egg-to-

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Table 1. Spawning population size, ova and fry production, adult returns, and fry-to-adult survival for naturally spawning Glenariffe Stream chinook salmon, 1965–1990.

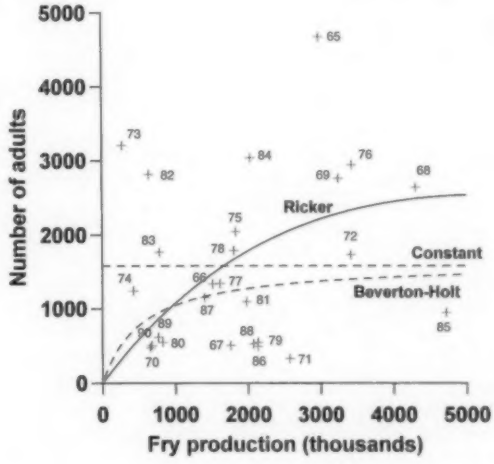
Brood year	Number of female spawners	Estimated ova deposited (thousands)	Estimated fry production (thousands)	Number of returning adults	% survival, fry to adult
1965	1278	6225	2988	4676	0.16
1966	573	3153	1513	1334	0.09
1967	746	3666	1760	505	0.03
1968	1781	8979	4310	2642	0.06
1969	1286	6768	3249	2760	0.08
1970	248	1365	655	474	0.07
1971	1084	5361	2573	330	0.01
1972	1618	7121	3418	1731	0.05
1973	160	725	275	3207	1.17
1974	173	851	426	1242	0.29
1975	799	3734	1834	2045	0.11
1976	1522	7158	3436	2943	0.09
1977	778	4066	1614	1341	0.08
1978	863	4773	1810	1787	0.10
1979	1413	7375	2138	546	0.03
1980	481	2387	826	548	0.07
1981	856	4121	1978	1097	0.06
1982	276	1339	643	2815	0.44
1983	326	1633	784	1766	0.23
1984	772	4243	2037	3037	0.15
1985	1800	9838	4722	950	0.02
1986	970	4449	2136	493	0.02
1987	669	2917	1400	1151	0.08
1988	838	4320	2074	526	0.03
1989	391	1598	767	615	0.08
1990	295	1409	676	504	0.07

Note: Fry production estimates for 1973–1976 are based on actual trap data (see text), while all other estimates are based on a mean egg-to-fry survival of 48%.

fry survival of 49.6%. This figure is consistent with the 1973–1976 figures (Table 1) and also supports the assumption that spawning success and egg-to-fry survival rates for spawners of natural and hatchery origin were comparable. I then used the average for all 5 years (48.0%) to derive estimates of the number of fry leaving Glenariffe Stream, based on the estimated ova deposition, for all years from 1965 to 1972 and from 1977 to 1990. From 1975 to 1980, a final adjustment to these estimates was made to allow for fry caught via the downstream trap and used to supply hatcheries and commercial salmon farms. This adjustment ranged from 49 000 fry in 1975 to 1.4 million fry in 1979. The mean weight of emergent fry trapped during 1973–1976 was approximately 0.3 g, and because 91–99% of the fry leaving Glenariffe Stream migrate within 24 h of emergence (Unwin 1986), I adopted this figure as the mean weight for all fry migrants.

Preliminary analysis of percentage survival rates for fish of both natural and hatchery origin (S_N and S_H, respectively) showed that the distribution of both parameters deviated considerably from normal, with pronounced skewness and kurtosis, but that log S_N and log S_H were normally distributed (Peterman 1981; Bradford 1995). Consequently, I used geometric rather than arithmetic means to characterise mean survival rates and derived nonsymmetric confidence intervals based on the log-transformed data. Stock–recruitment analysis for the naturally spawning population was carried out using the methods recommended by Hilborn and Walters (1992) to fit standard Ricker and Beverton–Holt models.

Fig. 1. Stock–recruitment scatterplot for naturally spawning chinook salmon in Glenariffe Stream, BYs 1965–1990. The 1973 datum was excluded when fitting the Beverton–Holt curve (see text).



Results

Natural runs

From 1965 to 1990, the number of female chinook salmon spawning in Glenariffe Stream ranged from 160 to 1800 and averaged 846. Estimated ova deposition ranged from 0.73 to 9.84 million and fry production from 0.28 to 4.72 million (Table 1). The number of spawners returning from each annual cohort ranged from 330 to 4676 and averaged 1579.

Fry-to-adult survival varied by nearly two orders of magnitude between years, from 0.013–1.17% (Table 1). The highest survival rates were for BYs 1973–1974 and 1982–1983, with the lowest survival rates for BYs 1971 and 1985–1986. Survival (log S_N) was uncorrelated with time ($r^2 = 0.004$, $p = 0.75$), with no evidence of any long-term trend over the 26 years of record. Mean survival was 0.079% (±95% confidence interval 0.053–0.116%). This represents a return of one adult per 1270 fry, or one pair of adults for every 2540 fry. Based on a mean output of 2376 fry per female spawner (Table 1), this is almost exactly equivalent to a return of one pair of adults for each spawning pair.

Stock size (as measured by annual fry production in thousands, F) and recruitment (as measured by adult returns, R) showed little evidence of any functional relationship (Fig. 1), and I could not reject the null hypothesis that R was uncorrelated with F ($p = 0.24$). Recruits per fry (as measured by log(R/F)) was therefore negatively correlated with F ($r^2 = 0.267$, $p < 0.01$), and I used this relationship to fit a Ricker model of the form $R = Fe^{a(1-F/b)}$ (Fig. 1). Parameter estimates for this model ($a = 0.256$, $b = 1371$) correspond to a maximum yield per recruit (e^a) of 1.29 adults per 1000 fry, or just over three returning adults per spawning pair. Although the model gives at best a poor fit to the data, with significant outliers in 1965, 1971, 1973, 1982, and 1985, it supports the conclusion that recruitment changes little with increasing stock size, particularly when annual fry production exceeds about 2 million. Attempts to fit a Beverton–Holt model of the form log(R) =

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Table 2. Raw and standardised (to 38 g release weight) survival rates for Glenariffe Stream hatchery chinook salmon, 1978–1990.

Brood year	Mean weight (g)	Release dates	Number of tag groups	Mean survival (%)	Standardised mean survival (%)
1978	14	Jan.–Aug.	5	0.46	1.58
1979	28	Dec.–Apr.	6	0.07	0.22
1980	11	Jan.–Apr.	5	0.05	0.29
1981	15	Jan.–Aug.	5	0.40	1.30
1982	24	Apr.–Aug.	40	0.58	1.35
1983	34	Mar.–Nov.	62	0.53	0.75
1984	49	Mar.–Oct.	31	0.41	0.32
1985	61	June–Aug.	15	0.17	0.10
1986	66	June–Aug.	7	0.22	0.13
1987	55	Mar.–Aug.	7	0.39	0.28
1988	51	Mar.–Aug.	8	0.27	0.19
1989	66	Mar.–Aug.	7	0.11	0.06
1990	40	Jan.–Aug.	11	0.11	0.29
1978–1990	38	Dec.–Nov.	209	0.34	0.33

$\log(aF/(b + F))$ failed, yielding a negative value (–73) for the parameter b and hence generating a discontinuous stock–recruitment curve that became infinite at $F = 73\,000$ fry. Refitting the model without the BY 1973 datum, which yielded a high level of recruitment from an unusually small spawning stock, yielded a nonpathological solution ($a = 1624$, $b = 524$) but did not give a convincing fit to the remaining data (Fig. 1).

Hatchery runs

Survival rates (S_H) for individual groups of coded-wire tagged hatchery-origin chinook released into Glenariffe Stream from 1978 to 1990 ranged from 0.008 to 3.28%, with a mean of 0.34% (95% confidence interval 0.30–0.40%). Interannual variation was less than for fry of natural origin, geometric mean annual survival rates ranging from 0.049% for BY 1980 to 0.58% for BY 1982 (Table 2).

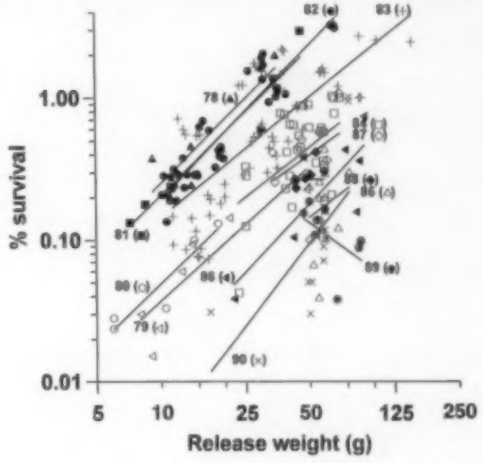
Comparison of survival rates between BYs was potentially confounded by interannual variation in mean release weight W (Table 2). To differentiate between BY and weight effects, I estimated the analysis of covariance (ANCOVA) model

$$\log S_{ij} = \mu_0 + \mu_1 \log W_{ij} + BY_j + \mu_2(BY_j \times \log W_{ij}) + \varepsilon_{ij}$$

to assess whether there was a significant interaction between BY and the covariate W, using the full data set of 209 release groups. Here, S_{ij} and W_{ij} are the individual survival and release weight measurements, μ_0 is the overall mean, μ_1 is the common (between BY) slope for regression of log S on log W, BY_j is the fixed BY effect, the term in μ_2 measures the interaction between BY and W, and ε_{ij} is the error term. I could not reject the null hypothesis that the coefficient of the interaction term (μ_2) was zero ($p = 0.47$), and hence concluded that the relationship between log S and log W was independent of BY. I then recalculated the above model, without the interaction term, to estimate the parameters μ_0, μ_1, and BY_j.

The fitted model gave a good fit to the data ($r^2 = 0.714$), confirming that survival varied consistently with release weight but also varied considerably between BY ($p < 0.001$ for both effects). The common slope coefficient μ_1 was 1.34, representing a 2.5-fold increase in S for each twofold increase in W. To facilitate comparisons between BYs, I estimated a "standardised" survival rate for each BY by calculating the expected survival rate at a release weight of 38 g, the mean release weight for all CWT groups. These estimates ranged from 1.58% for BY 1978 to 0.055% for BY 1989 (Table 2).

Fig. 2. $\log_{10}$(survival) versus $\log_{10}$(mean weight at release) for 209 groups of coded-wire tagged chinook salmon released from Glenariffe Hatchery, 1978–1990. Individual regression lines for each BY are superimposed. The projection of each line onto the horizontal axis indicates the range of release weights for each year.



Examination of individual linear regression relationships for log S on log W, for all 13 BYs from 1978 to 1990, confirms that the assumption of homogeneity of slopes is plausible (Fig. 2). With the exception of BY 1989, and to a lesser extent BY 1988, the tendency towards parallel slopes across all years is striking. The poor fit for 1988 and 1989 may be attributable to the relatively small range in mean release weight for releases in each of these 2 years, so that the respective regression relationships are poorly defined. In addition, the 1989 data correspond to tag recovery rates as low as two to five fish per release group and are thus subject to considerable statistical uncertainty. By contrast, survival data for the remaining 11 years conform strongly to the ANCOVA model, over release weights ranging from 6 g to at least 90–100 g.

Release dates from Glenariffe Hatchery covered a full 12-month period, from December in the first year of life (age 5 months) to the following November (age 16 months) (Table 2), although over 80% of releases took place between March and August (autumn and winter). I searched for a possible relationship between survival and release date by examining residuals from the above model. The residuals showed a weak negative correlation ($r^2 = 0.086$) with increasing release date, but this was strongly influenced by two relatively early (March–April) releases for BY 1983 and disappeared when these data were excluded from the regression. While a more detailed analysis, taking into account both size and time at release (e.g., Bilton et al. 1982; Ewing et al. 1984; Hemmingsen et al. 1986), may result in some adjustment of the standardised survival estimates listed in Table 2, I consider that any such changes would be small and of little relevance to the present study.

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Fig. 3. Annual survival rates for chinook salmon of natural and hatchery origin from Glenariffe Stream, 1965–1990.

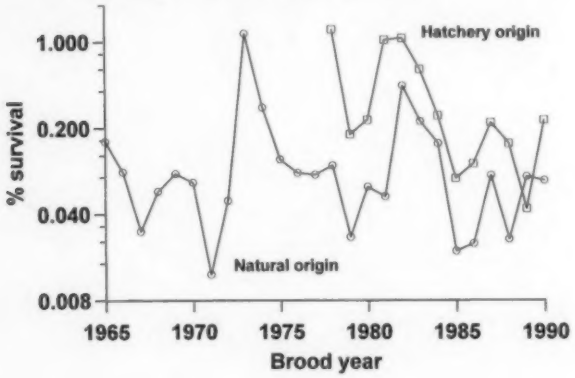
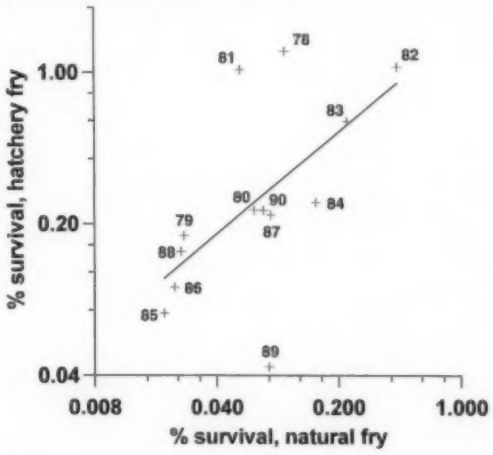


Fig. 4. Survival rates for chinook salmon of natural and hatchery origin from Glenariffe Stream, 1978–1990.



Survival rates for fish of natural and hatchery origin

The mean survival rate for hatchery fish (0.34%) was over four times greater than for naturally produced fry (0.079%). However, this comparison does not take into account the substantial difference in size between natural- and hatchery-origin fish when they leave Glenariffe Stream. The mean weight of emergent fry (0.3 g), which constitute 91–99% of the fry emigrating from Glenariffe Stream (Unwin 1986), is more than two orders of magnitude less than the mean weight at release for hatchery fish (38 g). Notwithstanding individual CWT groups of hatchery salmon that achieved survival rates exceeding 3%, the maximum survival rate for naturally produced fry (1.17%, BY 1973) was twice as high as the maximum annual mean (0.58%, BY 1982) for fish of hatchery origin.

Survival rates for naturally produced fry, and standardised survival rates for hatchery fish, followed similar annual trends (Fig. 3). Both populations were characterised by above-average survival rates during the early 1980s, a consistent and steady decline from 1982 to 1985, and a period of below-average survival from 1985 to 1990. The principal exceptions were 1978 and 1981, when hatchery survival rates were unusually high compared with naturally produced fish, and 1989, when hatchery survival rates were relatively poor. Excluding these outliers, survival rates for fish of natural and hatchery origin over the remaining 10 years of record were highly correlated (Fig. 4). Linear regression of log S_H on log S_N, for the full 13-year data set, yielded the relationship $\log S_H = 0.19 + 0.67 \log S_W$ ($r^2 = 0.36$, $p = 0.03$). Excluding the 1989 datum from this analysis (for the reasons discussed in the previous section) had little effect on the slope of the fitted regression line ($\log S_H = 0.30 + 0.70 \log S_W$; Fig. 4), but significantly improved the fit ($r^2 = 0.53$, $p = 0.007$).

Discussion

This study shows a striking discrepancy between fry-to-adult survival rates for naturally and hatchery-produced chinook originating from Glenariffe Stream. Survival rates for hatchery fish are, on average, four times higher than for naturally produced fry. However, this difference appears to be achieved only by virtue of their greatly increased size at release, as a result of extended freshwater rearing in the hatchery for 6–12 months. By contrast, survival estimates for the naturally spawning population are based on newly emerged fry, 92–98% of which leave Glenariffe Stream within 24 h (Unwin 1986). Although these results do not provide a direct measure of survival rates for naturally and hatchery-produced fish of equivalent size, the well-defined relationship between increasing release weight and survival for hatchery fish provides some basis for comparison. The mean survival rate for newly emerged fry weighing 0.3 g (0.08%) is attained by hatchery fish only when they reach an average size of 13 g, 40 times larger than their naturally produced counterparts.

Fry-to-adult survival rates for naturally produced chinook from any one cohort reflect the cumulative effects of mortalities over a life cycle of up to 4 years, with annually varying freshwater and marine components. Migration patterns of Rakaia River chinook conform to those typically displayed by North American fall-run chinook (Healey 1991), although both ocean- and stream-type juvenile life histories (Gilbert 1913; Healey 1983) are represented. Adults enter the river mouth during summer (January–February) and reach the headwater spawning grounds in autumn (April–May) (Flain 1982; Quinn and Unwin 1993). Fry hatch in spring (August–October), with 92–98% of these moving from Glenariffe Stream to the Rakaia River within 24 h of emergence, apparently in response to intense competition for rearing habitat (Unwin 1986). Some fry are presumably lost at this stage, particularly if the river is in flood, but significant numbers of fry successfully take up residence in the upper reaches, occupying the shallow water along the margins of the many braided channels that characterise the Rakaia and other Canterbury rivers (Glova et al. 1985; Hopkins and Unwin 1987).

During spring and summer (August–January), river-resident fry gradually disperse downstream, entering the ocean from November to January (Hopkins and Unwin 1987). Mortality rates during this migration are unknown. The Rakaia River has virtually no estuary (Eldon and Greager 1983), so that in contrast with most North American rivers (including the Sacramento), which provide significant intertidal rearing habitat (Healey 1982; Kjelson et al. 1982), Rakaia fry experience

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an extremely rapid transition from freshwater to seawater. Mean size at seawater entry for ocean-type fry (80 mm or 5 g; Hopkins and Unwin 1987; Unwin and Lucas 1993) is close to the 7-g mean weight required for successful acclimatisation of New Zealand chinook to salt water (Franklin et al. 1992), but significant mortalities almost certainly occur at this stage. Stream-type juveniles spend a full year in Glenariffe Stream and (or) the Rakaia River (Unwin 1986), entering the ocean at a mean size of 107 mm (Unwin and Lucas 1993). Yearlings make up less than 0.1% of the production from Glenariffe Stream and are also comparatively uncommon in the Rakaia River main stem (Hopkins and Unwin 1987). However, since stream-type adults constitute 38% of the returning population (Quinn and Unwin 1993), marine survival of stream-type fry must be relatively high.

Virtually nothing is known about the juvenile marine phase of New Zealand chinook, although yearling fish are taken in sheltered bays such as Akaroa Harbour, 60 km east of the Rakaia mouth (James and Unwin 1996). There is no commercial marine fishery for New Zealand chinook (McDowall 1994), and hence no data from which to estimate mortality rates (natural or otherwise) for adult chinook at ages 2, 3, and 4. Incidental landings of chinook by commercial trawlers increased between 1983 and 1988 and accounted for up to one third of the adults returning to freshwater in 1987 (Unwin et al. 1988*a*), but have now declined to insignificant levels (Unwin and James 1993). I did not adjust the return data to take account of catches at sea, so that survival estimates for BYs 1982 and 1983 (in particular) are conservative. My results also confirm that treating the annual interception rate for the freshwater sports fishery as constant is a reasonable approach in the context of the present study. While this assumption is unlikely to be strictly true, the effect of a moderate (e.g., 10–20%) interannual variation in angler catch rate would be small compared with the nearly 100-fold variation in survival rate and would become important only if there were a substantial difference between catchability of natural and hatchery chinook.

In contrast with naturally produced fry, hatchery chinook released from Glenariffe Stream appear to travel down the Rakaia River relatively quickly, passing through the lower reaches within a few days of release (Unwin et al. 1989). SPA confirms that hatchery fish spend little time (typically less than 2 weeks) in riverine freshwater habitats before entering the ocean, particularly for release dates between March and August (Unwin and Lucas 1993). Annual variability in survival rates for hatchery fish is therefore likely to reflect marine rather than freshwater influences. Although survival rates for fish of natural and hatchery origin are likely to differ due to factors such as increased vulnerability to predation among hatchery (or "naive") fish (cf. Healey and Reinhardt 1995), the present results suggest that once allowance is made for interannual variation in weight at release for hatchery fish, the difference is relatively constant from year to year.

The parallel trend in survival rates for natural- and hatchery-origin chinook from Glenariffe Stream over a 13-year period therefore strongly suggests a common, marine influence and implies that interannual variability in survival rates for naturally produced fish is also controlled by marine rather than freshwater factors. If so, the tendency for mortalities from sources such as predation and (or) competition for food and habitat to decrease with increasing fish size (e.g., Parker 1962; Marschall and Crowder 1995) suggests that the critical processes governing BY survival occur relatively early during the juvenile marine phase of the life cycle. The crucial period may be the first winter at sea, early enough for naturally produced juveniles still to be vulnerable but not so early that hatchery fish released in autumn and winter are no longer susceptible.

The flat stock–recruitment relationship for Glenariffe Stream chinook strongly suggests some form of density dependence. Although the relationship between stock and recruitment is poorly defined, recruitment appears to increase very rapidly when stock size is small, with little or no further increase once stock size exceeds about 0.5 million fry. The mechanisms responsible for this trend are open to speculation. Density-dependent survival in anadromous salmonids can often be attributed to freshwater limitations associated with competition for spawning habitat (Hilborn and Walters 1992), but this does not appear to be the case in Glenariffe Stream where egg-to-fry survival is approximately constant for spawning populations ranging from 160 to 1522 females (Unwin 1986). The mass migration of fry from Glenariffe Stream into the Rakaia River, within 24 h of emergence, probably indicates that rearing habitat in Glenariffe Stream is limiting (Unwin 1986), although it is also possible that natal stream rearing was never part of the evolutionary strategy of the ancestral Sacramento subpopulation. There are no data on whether mortality within the Rakaia River is density dependent. However, there appears to be an abundance of rearing habitat within the braided channels of the lower Rakaia (Glova and Duncan 1985), so that rearing capacity is very much greater than for Glenariffe Stream (Hopkins and Unwin 1987). Given that BY survival for Glenariffe Stream chinook appears to be related to marine rather than freshwater influences, during the first year of life, density dependence within the inshore marine environment may be significant. If so, BY survival may be highly sensitive to annually varying factors within this environment, producing the extreme variability apparent for Glenariffe Stream chinook. There is increasing evidence that BY survival rates for anadromous salmon within the Pacific Northwest are linked to climatic and environmental processes such as El Niño (Johnson 1988), and there is considerable scope for similar studies on New Zealand chinook.

The discrepancy between survival rates for natural and hatchery chinook from Glenariffe Stream is highlighted by the need for "delayed" releases, at ages of 8–12 months, to achieve even a modest return. At Glenariffe, as at other New Zealand hatcheries, the policy of delayed releases evolved in response to consistently poor returns from more traditional releases of "90-day fingerlings" as usually practiced in North America. For example, survival rates for fall chinook released from 20 Columbia River hatcheries, typically at weights of 5–10 g, averaged 0.33% for BYs 1979–1981 (Vreeland 1989). Releases of chinook fry from the Snootli Creek and Kitimat River Hatcheries in British Columbia, Canada, at weights of 3–10 g, yielded survival rates of 0.26 and 0.46% (excluding the in-river sport catch), respectively (Winton and Hilborn 1994). However, releases of fish <10 g from New Zealand hatcheries have, almost without exception, been total failures. Of 48 groups of coded-wire tagged fish released into seven east coast rivers between 1977 and 1981, totalling 517 000 fry at weights of 4–10 g, only four groups yielded returns exceeding 0.05%, with 30 groups producing a nil return (Unwin et al. 1988*b*).

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These releases involved five distinct hatchery sites, using a range of different incubation and rearing techniques, suggesting that the weak returns were not simply the result of poor husbandry. By contrast, an experimental release of 35-g yearling fish in 1979 yielded a 2.6% return and was followed by a 5.1% return from a similar release in 1981. As a result of these successes, delayed releases became standard practice at virtually all hatcheries after 1981. Of interest is that the original liberations of Sacramento fish from the Hakataramea Hatchery (McDowall 1995) also involved yearling and older releases. Contemporary hatchery records do not give precise release dates, but age at release ranged from 3 to at least 26 months, with several groups released as "yearlings" in December (midsummer), 1 year after their arrival from the United States the preceding January (Anonymous 1901–1907).

Although delayed releases increased survival rates, their consequences in terms of other life history traits and (or) physiological responses are unknown. Autumn and winter are the times of minimum downriver migration among Rakaia River chinook, representing a gap between the last ocean-type fry leaving the river mouth in late summer (Hopkins and Unwin 1987; Unwin and Lucas 1993) and peak migration of yearling stream-type fish the following spring (Unwin 1986). New Zealand chinook can successfully adapt to seawater in autumn and winter at weights of 50–70 g (Franklin et al. 1992), but high straying rates for Glenariffe hatchery chinook released between May and August indicate that at least one behavioural response, i.e., homing, is impaired by off-season releases (Unwin and Quinn 1993). In New Zealand chinook, migration timing and date of seawater entry are presumably responding to seasonal availability of suitable food items and (or) the presence of likely marine predator species such as kahawai (*Arripis trutta*). Little is known about the marine diet of juvenile chinook in New Zealand waters other than that yearling chinook captured in sheltered bays near the Rakaia River mouth feed opportunistically on larval fish and crustaceans, principally mysids (James and Unwin 1996), and it is possible that survival rates after seawater entry may be limited by prey abundance.

A corollary of the above arguments is that for naturally produced fry, first-year mortality in freshwater may be relatively unimportant in determining BY survival. This is consistent with a recent comparative study of survival rates for Pacific salmon (Bradford 1995), which concludes that freshwater survival rates for chinook are the highest of any Pacific salmonid, and suggests that marine survival may be correspondingly low. My findings also contrast with an earlier study of Rakaia River chinook, which concluded that most emergent fry from Glenariffe Stream were unable to maintain residence in the Rakaia River (particularly during spring floods) and were thus too small to survive the transition to seawater (Flain 1982). In one form or another, this view has dominated management of the New Zealand salmon fishery for the last 20–30 years, an implicit assumption behind the development of commercial hatcheries during the 1980s being that chinook stocks were limited primarily by availability of freshwater habitat (McDowall 1994). The present study suggests that hatchery releases may in fact be of little value in increasing total salmon production much beyond current levels. Run strength in Glenariffe Stream has not increased since hatchery releases were initiated, but naturally spawning stocks have declined (Unwin and Glova 1997), suggesting that hatchery fish have replaced naturally spawning fish rather than supplementing them. This is reminiscent of experiences such as the Canadian Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement programme where, despite increased fry production from artificial spawning channels, adult returns did not respond (McDonald and Hume 1984). Poor survival rates for Glenariffe chinook during the late 1980s coincided with the period when output from commercial hatcheries peaked at over 6 million fish annually (Unwin 1991) and are consistent with marine survival being density dependent. It is interesting to note that during a visit in 1926, Charles Gilbert (Stanford University), one of the leading fisheries biologists of the day, cautioned against commercial fishing until salmon were thoroughly established in New Zealand (McDowall 1994).

More generally, these results suggest that any attempts to significantly increase New Zealand chinook stocks, whether by stream improvement, angler harvest regulations, or ova planting, may have limited potential. If so, fishery managers need to recognise this by developing management objectives that are appropriate and achievable. The most consistently successful releases of hatchery fish in recent years have been small-scale (<50 000 annually), well-targeted releases from locations such as Otago Harbour (Walton 1991) and Silverstream (a small spring-fed stream on the outskirts of Christchurch; NIWA, unpublished data). All of the Silverstream releases, and some of the Otago Harbour releases, comprised fish initially reared at Glenariffe and trucked to their final release location, giving further support to the conclusion that the inconsistent returns to Glenariffe were not simply due to poor hatchery technique. In both cases, adult returns have generated lively "minifisheries" in waters not normally populated by salmon, bringing significant benefits to local anglers. Release programmes such as these, where the number of fish involved is small compared with the total New Zealand stock but large enough to sustain a local sports fishery, may have considerable potential.

In summary, the present study clearly demonstrates that fry-to-adult survival rates for hatchery-reared chinook released from Glenariffe Stream fall well short of what would be expected given their great size advantage over naturally produced fry. To the extent that naturally produced fry can be considered "wild", this result provides an example in which hatchery fish may have a lower "fitness to survive" than wild fish (e.g., Hindar et al. 1991; Waples 1991). However, the hatchery release strategy used at Glenariffe is unusual from a North American perspective and precludes a more direct comparison with other results for chinook salmon within their native range. Implementation of similar comparative studies in the Pacific Northwest would help to clarify the biological processes that determine fitness to survive, both in New Zealand and in North America.

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Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs

R.L. France and R.H. Peters

Abstract: Data from 35 published studies were collated to examine patterns in the trophic enrichment of ^{13}C of consumers. Because both $\delta^{13}C$ and $\delta^{14}N$ vary systematically across ecosystems, it was necessary to standardize for such differences before combining data from numerous sources. Relationships of these measures of ecosystem-standardized $\delta^{13}C$ to ecosystem-standardized trophic position ($\Delta\delta^{15}N$) for freshwater, estuarine, coastal, and open-ocean and for all aquatic ecosystems yielded regression equations of low predictive capability (average of 20% explained variance in $\delta^{13}C$). However, differences were observed in the slopes between $\delta^{13}C$ and standardized trophic position when data were examined study-specifically: the average trophic fractionation of ^{13}C was found to increase from +0.2‰ for freshwater to +0.5‰ for estuarine to +0.8‰ for coastal, and to +1.1‰ for open-ocean food webs. This ecosystem-specific gradient in ^{13}C enrichment for consumers supports previous findings of a similar continuum existing for zooplankton – particulate organic matter differences in $\delta^{13}C$. Possible mechanisms to explain these ecosystem-specific patterns in ^{13}C enrichment may be related to the relative importance of detritus, heterotrophic respiration, partial reliance on alternative food sources, and lipid influences in the different ecosystems.

Résumé : Les données de 35 études publiées ont été rassemblées pour examiner les modalités de l'enrichissement trophique en ^{13}C des consommateurs. Comme le $\delta^{13}C$ et le $\delta^{14}N$ varient tous deux systématiquement d'un écosystème à l'autre, il a été nécessaire de normaliser avant de combiner les donner de nombreuses sources. Les relations de ces mesures du $\delta^{13}C$ normalisés en fonction de l'écosystème à la position trophique normalisée en fonction de l'écosystème ($\Delta\delta^{15}N$) pour l'eau douce, les eaux estuariennes, les eaux côtières et l'eau de mer au large et pour tous les écosystèmes aquatiques ont donné des équations de régression de faible valeur prédictive (moyenne de variance expliquée de 20% pour le $\delta^{13}C$). Cependant, des différences ont été observées dans les pentes entre le $\delta^{13}C$ et la position trophique normalisée lorsque les données étaient examinées de manière spécifique de l'étude : on a constaté que le fractionnement trophique moyen du ^{13}C a augmenté de +0,2‰ pour les réseaux trophiques d'eau douce à +0,5‰ dans les eaux estuariennes à +0,8‰ dans les eaux côtières et à +1,1‰ dans l'eau de mer au large. Ce gradient spécifique de l'écosystème dans l'enrichissement trophique en ^{13}C des consommateurs vient appuyer les constatations antérieures d'un continuum semblable dans le cas des différences zooplancton – particules organiques en $\delta^{13}C$. Les mécanismes possibles expliquant ces variations spécifiques de l'écosystème dans l'enrichissement en ^{13}C peuvent être liés à l'importance relative des détritus, de la respiration hétérotrophe, du recours partiel à des sources alimentaires de substitution et des effets des lipides dans les différents écosystèmes.
[Traduit par la Rédaction]

Introduction

As a result of differential fractionation during food assimilation, ^{15}N becomes enriched over ^{14}N (DeNiro and Epstein 1981) such that the ratio between the two isotopes expressed in relation to the analytical standard (i.e., $\delta^{15}N$) increases between 3 and 4‰ with each successive trophic category (e.g., Owens 1987). Likewise, ^{13}C becomes enriched over ^{12}C during food assimilation (DeNiro and Epstein 1978), leading some to suggest that a trophic increase in $\delta^{13}C$ should also occur in food webs (e.g., McConnaughey and McRoy 1979; Rau et al. 1983; Fry et al. 1984; Mills et al. 1984; Rodelli et al. 1984; Monteiro et al. 1991; Sholto-Douglas et al. 1991). The lack of any consistency, however, in the ^{13}C-enrichment factors reported among the various studies (ranging from +0 to +1.5‰) led Fry and Sherr (1984) to conclude that it is "difficult to model food web structure using $\delta^{13}C$ data", despite the fact that "establishing the exact magnitude of the ^{13}C increase can be quite important if accurate corrections are to be made in [food source] mixing models". More recent studies that have measured the actual trophic position of individual organisms through $\delta^{15}N$ analysis have continued to generate mixed results as to whether or not any progressive ^{13}C enrichment develops in aquatic food webs (e.g., Dickson 1986; Wada et al. 1987; Fry 1988; Hobson and Welch 1992; France 1995*a*, 1996; Keough et al. 1996).

The purpose of the present study was to collate the extant dual-isotope data ($\delta^{15}N$ and $\delta^{13}C$) from aquatic systems to determine if empirical relationships exist between these isotopes that transcend individual studies such that a general trophic fractionation of ^{13}C could be predicted. Because such empirical relationships were not found, however, among data pooled from different studies, we then examined whether ecosystem differences existed in ^{13}C enrichment within specific studies.

Methods

Because $\delta^{15}N$ values at the base of food webs vary across different ecosystems (France 1995*b*), it was necessary to standardize among

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Fig. 1. Scattergram of ecosystem-standardized $\delta^{13}C$ ($\Delta\delta^{13}C$) against ecosystem-standardized trophic position ($\Delta\delta^{15}N$) for consumers from all aquatic food webs.

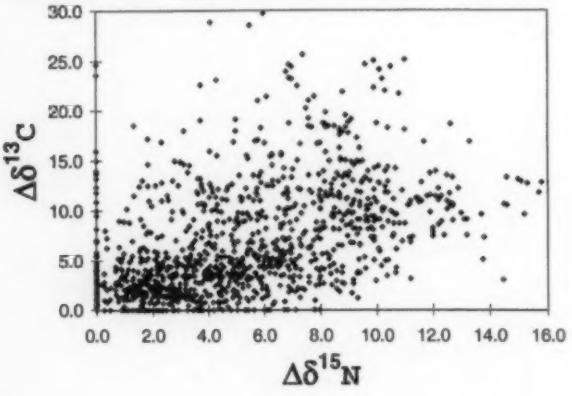
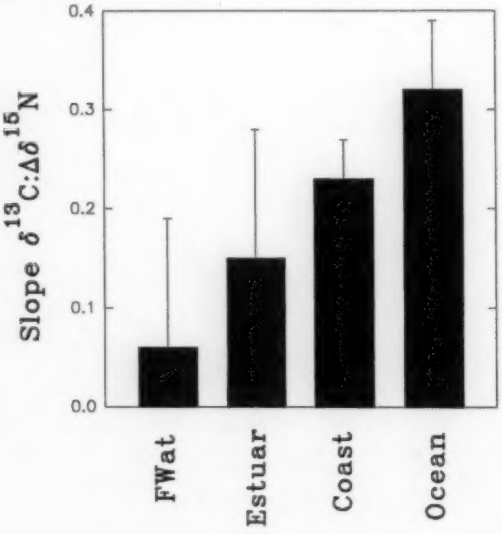
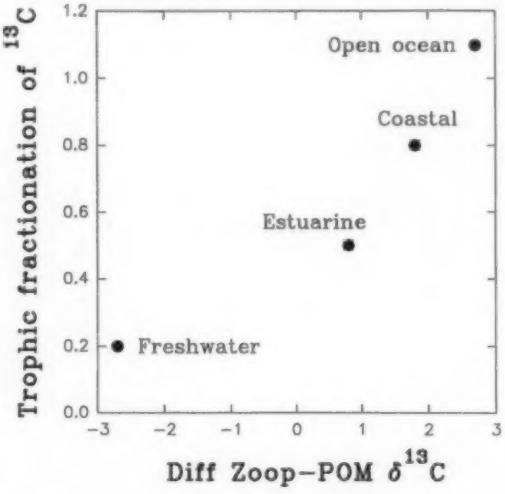


Fig. 2. Average (+SE) of study-specific slopes between $\delta^{13}C$ and standardized trophic position ($\Delta\delta^{15}N$) grouped across ecosystem categories.



studies. We accomplished this by simply expressing consumer trophic positions as increases in $\delta^{15}N$ from that of the average for the three lowest measurements found for herbivores within each individual study system. Such an approach will remove proportional among-study differences in the extent of ecotonal coupling between terrestrial and freshwater (France 1997), terrestrial and estuarine (R.L. France, unpublished data), and freshwater and marine (Peterson et al., cited in France 1994; Hesslein et al. and Sullivan and Moncreiff, cited in France 1995*c*) environments, as well as to correct for differences in the occurrence of nitrogen fixation (Shearer and Kohl 1989) and anthropogenic inputs (Macko and Ostrom 1994). Similarly, because $\delta^{13}C$ at the base of food webs varies across different ecosystems (Fry and Sherr 1984), it was also necessary to standardize these values among studies in a similar manner as for $\delta^{15}N$. In total, 1401 paired data points (675 freshwater, 323 estuarine, 206 coastal, and 196 open ocean) for consumers were obtained from 35 different studies.[1]

Fig. 3. Ecosystem-specific pattern in the trophic enrichment of ^{13}C (assuming an average trophic enrichment of 3.5‰ in $\delta^{15}N$, Owens 1987) in relation to differences in $\delta^{13}C$ between zooplankton and POM from del Giorgio and France (1996).



Results and discussion

The relationship of standardized $\delta^{13}C$ to standardized trophic position for consumers from all ecosystems (Fig. 1), although significant, yielded a very weak predictive capability (R^2 = 0.24). Similarly, compartmentalizing the data into freshwater, estuarine, coastal, and open-ocean ecosystems did not substantially improve the predictive capabilities: coefficients of determination were higher for estuarine and coastal consumers (R^2 = 0.25 and 0.31) than for freshwater and open ocean consumers (R^2 = 0.10 and 0.13), suggesting the possibility of transecotonal foraging by mobile animals in the former environments with the consequent shifts in both isotope signatures (cf. France 1995*c*). This lack of cross-study predictive equations is obviously a severe limitation toward development of any general ^{13}C-enrichment factor.

The average slopes between $\delta^{13}C$ and standardized $\delta^{15}N$ for consumers from individual studies increased progressively from freshwater to estuarine to coastal to open-ocean ecosystems (Fig. 2). These data translate into average trophic ^{13}C enrichments of +0.2‰ for freshwater food webs, +0.5‰ for estuarine food webs, +0.8‰ for coastal marine food webs, and +1.1‰ for open-ocean food webs (Fig. 3). The pattern shown here for herbivores to top-level consumers matched the continuum in ^{13}C differences observed previously (del Giorgio and France 1996) between zooplankton and particulate organic matter (POM) across these same ecosystem categories (Fig. 3).

del Giorgio and France (1996) interpreted the ecosystem-specific patterns in ^{13}C enrichment between zooplankton and

[1] A complete set of tabular data may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2.

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POM as being due to the degree of POM dilution by nonalgal sources of organic carbon as well as the possibility of depth-related changes in the isotopic signature of phytoplankton resulting from heterotrophic respiration. The present secondary analysis of ^{13}C enrichment for consumers supports the previous contention of systematic differences existing in the pathways of organic carbon flow among aquatic ecosystems. Foraging across isotopically distinct habitat boundaries will obscure isotopic relationships between consumers and food sources and can be expected to be greater in freshwaters and estuaries than in coastal zones, and may be almost absent in the open ocean (del Giorgio and France 1996). As a result, only data from marine food webs conform to the laboratory predictions (DeNiro and Epstein 1978) of a ^{13}C enrichment of about +1‰ per trophic category that Fry and Sherr (1984) concluded would "suffice" for most purposes with respect to tracing material flow. Consequently, earlier conclusions made for oligotrophic Canadian Shield lakes (France 1996) that "it is probably wisest to interpret dietary pathways inferred from field research directly with no systematic and cumulative trophic fractionations of ^{13}C taking place" are not merely idiosyncratic for these systems but instead hold for freshwater food webs in general. As a result, a priori adjustments in $\delta^{13}C$ made by some researchers (cited in France 1995*a*, 1996) examining freshwater and estuarine organisms to accommodate for trophic enrichments that are believed to occur based on data from marine food webs may be inappropriate.

Less than 5% of the data used in our analyses derive from lipid-extracted measurements which could conceivably produce differences in $\delta^{13}C$ determinations (DeNiro and Epstein 1977). The overall influence of lipids on food-web patterns of $\delta^{13}C$ remains unclear. Analytical extractions or empirical corrections have suggested that organismal differences in lipid content may be important in some (Wada et al. 1987; Rau et al. 1991, 1992) but not all (Hobson and Welch 1992) polar open oceans, and not in some oligotrophic Canadian Shield lakes (France 1995*a*, 1996) in terms of $\delta^{13}C$ values. Obviously, future research needs to examine just how, if any, systematic trophic position differences in lipid content may regulate ^{13}C enrichment.

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With warm dedication to the memory of Rob Peters who, never satisfied with the idiosyncrasies of site-specific, individual-effort research, always stressed the importance and need of searching for general patterns across all systems through the use of as much of the extant data from the literature as possible. C. Rigg helped with the analysis of the particluar data used here.

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Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A.

Mark S. Wipfli

Abstract: Terrestrial-derived invertebrate (TI) inputs into streams and predation on them by salmonids (40–180 mm fork length) were measured in six coastal Alaska stream reaches from April through October 1993–1994; riparian habitat of three stream reaches contained conifer-dominated old-growth (no timber harvesting) and three were alder-dominated young-growth (31 years postclearcutting). Data from pan-traps placed on stream surfaces showed that TI biomass and nitrogen inputs averaged up to 66 and 6 $mg \cdot m^{-2} \cdot day^{-1}$, respectively, with no significant difference between habitats. Stomach contents from coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*O. clarki*), and Dolly Varden (*Salvelinus malma*) revealed that TI and aquatic-derived invertebrates (AI) were equally important prey. Additionally, salmonids from young-growth systems ingested a greater TI proportion than those from old-growth systems. There were trends but no significant differences between habitats of TI and AI biomass ingested; however, statistical power was <0.30. These results showed that TI were important juvenile salmonid prey and that a riparian overstory with more alder and denser shrub understory may increase their abundance. Riparian vegetation management will likely have important consequences on trophic levels supporting predators, including but not limited to fishes.

Résumé : Les apports d'invertébrés d'origine terrestre (IT) dans les cours d'eau et la prédation exercée sur eux par les salmonidés (longueur à la fourche de 40–180 mm) ont été mesurés dans six tronçons de cours d'eau côtiers de l'Alaska d'avril à octobre 1993–1994; les habitats riverains de trois des tronçons de cours d'eau étaient constitués de forêts mûres (absence de récolte du bois) dominées par des conifères et les trois autres étaient constituées de jeunes forêts (31 ans depuis la coupe à blanc) dominées par l'aulne. Les données obtenues grâce à des pièges à eau placés à la surface des cours d'eau ont montré que la biomasse d'IT et les apports en azote s'élevaient en moyenne à 66 et 6 $mg \cdot m^{-2} \cdot jour^{-1}$, respectivement, sans qu'il y ait de différences statistiquement significatives entre les habitats. Le contenu stomacal de saumons coho (*Oncorhynchus kisutch*), de truites fardées (*O. clarki*) et de Dolly Varden (*Salvelinus malma*) a révélé que les IT et les invertébrés d'origine aquatique (IA) étaient des proies d'égale importance. De plus, les salmonidés des systèmes de jeunes forêts ingéraient une proportion plus grande d'IT que ceux des systèmes de forêts mûres. Il y avait des tendances, mais non des différences significatives, entre les habitats pour ce qui est de la biomasse d'IT et d'IA ingérés; cependant, la puissance statistique était <0,30. Ces résultats ont montré que les IT étaient des proies importantes pour les salmonidés juvéniles et qu'un étage dominant riverain contenant plus d'aulnes et un sous-étage d'arbustes plus denses peuvent accroître leur abondance. La gestion de la végétation riveraine aura vraisemblablement des conséquences importantes sur les niveaux trophiques qui soutiennent les prédateurs, y compris mais non exclusivement les poissons.
[Traduit par la Rédaction]

Introduction

Riparian zones play a major role in regulating nutrient and energy flow in low-order streams (Webster and Benfield 1986; Cummins et al. 1989; Webster et al. 1992). Leaf litter and wood originating from riparian vegetation enters the lotic system and affects associated microbial and benthic macroinvertebrate communities that consume and process this organic material (Sedell et al. 1975; Vannote et al. 1980; Cummins et al. 1989; Hax and Golladay 1993). This allochthonous material typically constitutes the energy base in low-order forested streams (Minshall 1967; Fisher and Likens 1973; Triska et al. 1982).

While it is understood that stream ecosystems are closely linked to and dependent on their associated riparian zones for organic matter and nutrient inputs, little attention has focused on the terrestrial invertebrate communities associated with riparian vegetation and on how these plants influence terrestrial invertebrates entering streams (e.g., as prey for predators, or as allochthonous material contributing nutrients and organic matter). Southwood (1961) reported that deciduous trees generally have more associated invertebrate species than do conifers. Plant community successional stage also plays a variable role in the associated invertebrate community dynamics by regulating their abundance and species assemblage (Mispagel and Rose 1978). Schowalter et al. (1981) reported lower arthropod mass 1 year after clearcutting but higher mass 2 year

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postclearcutting, relative to an uncut forest. Mundie (1974) indicated that aerial insects were more abundant in a deforested than forested setting in coastal British Columbia, Canada, and that terrestrial insects may be seasonally important salmonid food. Some riparian tree species contribute more terrestrial invertebrate mass to streams than others (Mason and Macdonald 1982).

Little consideration has been given to the role of terrestrial invertebrates in aquatic food web ecology and dynamics, even though their occurrence in fish diets is well documented (Sterba 1962; Hynes 1972; Scott and Crossman 1973; Maitland 1977; Garman 1991). Terrestrial invertebrates often comprise more than 50% of juvenile salmonid diets and associated energy intake during certain times of the year and are often a preferred prey (reviewed by Hunt 1975). Nielsen (1992) reported that the energy contribution of terrestrially derived prey represented from 15 to 28% of the total energy intake for juvenile coho salmon (*Oncorhynchus kisutch*) during summer in a Washington stream. Cada et al. (1987) stated that terrestrial prey were more common in trout stomachs than in the drift, fish had a preference for terrestrial prey over aquatic prey, and riparian vegetation was an important prey source. Cadwallader et al. (1980) indicated that overhanging vegetation was important for terrestrial invertebrate inputs in some Victorian streams and terrestrial prey were more common in diets of fish from sites with overhanging vegetation.

If riparian communities govern terrestrial invertebrate inputs, then riparian management activities that alter plant communities may change food resources within and surrounding the stream. Timber clearcutting in southeastern Alaska across riparian zones of salmonid-rearing streams (pre-1990 timber harvest practices) has given rise to even-aged young-growth riparian communities of various successional stages. Red alder (*Alnus rubra*) often dominates riparian regrowth canopies with variable amounts of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), in addition to some western redcedar (*Thuja plicata*), Alaska yellow-cedar (*Chamaecyparis nootkatensis*), black cottonwood (*Populus trichocarpa*), and willow (*Salix* spp.) in some areas. Influence of these developing riparian communities on stream productivity and fisheries, including energy pathways via terrestrial invertebrate inputs, is unknown. Maintaining productive salmonid fisheries in southeastern Alaska is critical to the economy and quality of life of peoples of this region; preserving riparian and stream productivity is essential for sustaining this resource. Understanding the role of terrestrial invertebrates in stream food webs and how riparian habitat types influence their inputs into streams is crucial for managing these riparian–stream ecotones.

The objectives of this study were to (*i*) measure terrestrial-derived invertebrate (TI) inputs into streams and predation on them by salmonids (40–180 mm fork length) in six Alaska temperate rainforest stream reaches from April through October 1993–1994 and (*ii*) contrast these responses between streams containing conifer-dominated old-growth (little to no timber harvesting) riparian habitat and alder-dominated young-growth (31 years postclearcutting) riparian habitat. TI inputs were assessed in terms of biomass and nitrogen they contributed to streams, and predation on them by comparing biomass of TI versus aquatic-derived invertebrates (AI) consumed by salmonids.

Methods

Study site

The study took place on Revillagigedo Island located within the Alexander Archipelago temperate rainforest of the southeastern Alaska panhandle. Climate is maritime: cool and moist; precipitation can exceed 500 cm·year^{-1} in some areas (Harris et al. 1974).

The study was conducted May–October 1993 and April–May 1994 at Bear, Cedar, Cobble, Spike, Upper Sprout, and Lower Sprout creeks (informally named for study purposes) within or near the 22.6-km^2 Margaret Lake catchment (55°41′N, 131°36′W) on Revillagigedo Island, Alaska, U.S.A. (Fig. 1). Riparian canopies (mostly closed) contained Sitka spruce, western hemlock, western redcedar, and red alder. Riparian areas of Bear and Sprout creeks contained 31-year-old regrowth of alder or alder–spruce mix; those of Cedar, Cobble, and Spike creeks contained conifer-dominated old-growth canopies. Study reaches of Cedar and Spike creeks were fully contained within old-growth riparian areas. Also, a logging road paralleled Spike Creek 50–100 m away. The Cobble Creek site contained old-growth riparian habitat except for roughly one quarter of its length that received some timber harvesting up to 30 m from the stream banks 30 years earlier. Sprout Creek contained two study reaches with distinctly different riparian habitats: alder-dominated closed-canopy and a partially open mixed alder–spruce canopy. Remaining streams contained single study reaches. Understories were mixtures of blueberry (*Vaccinium ovalifolium* and *V. alaskaense*), salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*), and elderberry (*Sambucus racemosa*) with other occasional species. Young-growth understories were more dense than those of the old-growth communities (Table 1). Stream channels averaged 2–9 m wide, were generally unrestricted, and contained sand to boulder-sized substrata with frequent coarse woody debris (CWD). Study reaches ranged from 60 to 200 m long with <5% gradients.

Stream inputs of terrestrial invertbrates

To assess the importance of TI as allochthonous input, I measured number and biomass and determined taxonomic composition of TI and nonwoody plant mass and composition entering streams. Invertebrates were categorized as terrestrial (terrestrially derived) if they were a product of terrestrial secondary production (i.e., terrestrial stages of aquatic production were not classified as TI). The null hypothesis for comparing habitats was that the quantity of TI entering streams was similar between habitats.

Five dark-colored floating pan-traps (930-cm^2 surface area with 13-cm-high sides) containing ~5 mL of dish soap and 2 L of stream water were placed on stream-water surfaces within each study reach. Traps were approximately evenly spaced and haphazardly placed on pool surfaces throughout stream reaches. The soap helped preserve trap contents and reduced water surface tension within the traps to help retain invertebrates. Traps were designed to catch plant litter and invertebrates landing on the stream surface. Traps were tethered with nylon cord to overhanging tree limbs or other structures and were not positioned according to distance from stream banks.

Trap contents were collected up to every 2 weeks. Invertebrates visible to the unaided eye were removed and remaining nonwoody plant material was strained through a 105-µm-mesh sieve. Invertebrates were placed into 70% EtOH within plastic bags and taken to the laboratory to identify, count, and determine mass. I identified all invertebrates to Order, or Family if necessary, recorded body lengths to the nearest 1 mm, and calculated dry masses with published taxon-specific length–mass conversion equations (Rogers et al. 1976, 1977; Smock 1980). I used these equations because they provided more accurate measurements of original invertebrate mass than did direct weighing of preserved specimens (Meyer 1989), and specimens may have lost mass due to partial decomposition while in traps. Nonwoody plant material was placed into paper envelopes, oven dried, separated into categories (coniferous, alder, nonalder deciduous), and then

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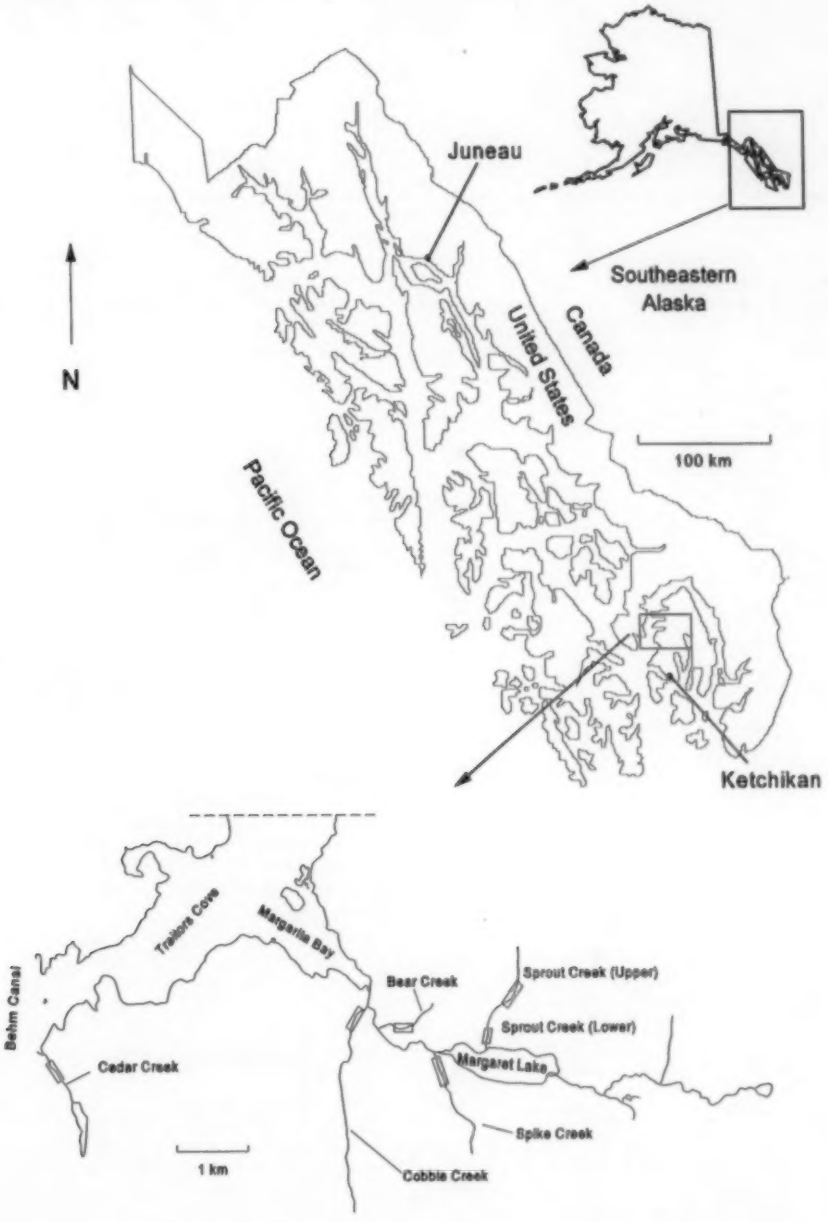
Fig. 1. Rectangles enclosing selected stream reaches on bottom map show approximate TI input and salmonid diet study locations during 1993 and 1994 in southeastern Alaska.



ashed to estimate ash-free dry mass (AFDM). I assumed that leaf mass loss due to leaching in trap water was similar to published rates and used published means for coniferous (Short et al. 1980), alder (Kaushik and Hynes 1971; Triska and Sedell 1976; Short et al. 1980), and other deciduous species (Kaushik and Hynes 1971) to correct measured values. Published mean nitrogen content values were used to estimate the amount of nitrogen entering streams via invertebrates and plant litter (Table 2).

Terrestrial invertbrates as salmonid prey

To determine if TI were an important component of these stream food webs through contributing to predatory fish diets, I compared number and mass of TI versus AI prey ingested by salmonids monthly from May through October 1993. Salmonids 40–180 mm fork length were captured using "minnow" traps (42 cm long × 23 cm wide), each containing a perforated 7 × 17 cm plastic bag of salmon eggs as bait. Traps were placed in nonriffle habitats >25 cm deep. Fishes present were coho salmon, cutthroat trout (*Oncorhynchus clarki*), steelhead (*O. mykiss*), Dolly Varden (*Salvelinus malma*), and sculpin (*Cottus* spp.) at various compositions. Sculpin and the relatively uncommon steelhead were excluded from analyses. Traps remained in streams about 1 h. Collected fish were placed in 20-L buckets of

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Table 1. Study site characteristics.

Stream	Riparian habitat[a]	Study reach length (m)	Stream width (m)[b]	Canopy composition[c]	Understory composition[d]	Understory density[e]
Cedar Cr.	OG	85	2.6±0.2	H≡C>S>A	BB>DC>SB	L
Cobble Cr.	OG	160	8.6±0.9	H>S>A[f]>C	BB>SB>DC	M
Spike Cr.	OG	200	5.3±0.4	H>S>C>A[f]	BB>DC>SB	M
Bear Cr.	YG	75	2.1±0.3	A≡S>H>C	SB>BB>DC	H
Lower Sprout Cr.	YG	60	2.6±0.3	A⋗S>H>C	SB>BB>DC	H
Upper Sprout Cr.	YG	90	2.5±0.2	A≡S>H>C	SB>BB>DC	H

[a]OG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.
[b]Mean ± SE.
[c]Dominant species in order of abundance based on visually estimated foliage composition of trees with stems within 30 m of permanent stream banks: A, alder; C, cedar; H, hemlock; S, spruce.
[d]Dominant species in order of abundance based on visually estimated foliage composition of the three most common understory shrub species: BB, blueberry; DC, devil's club; SB, salmonberry.
[e]Relative shrub density comparison among six sites: L, low; M, medium; H, high.
[f]Riparian canopy also contained frequent subdominant alder.

Table 2. Nitrogen levels of invertebrate and leaf[a] tissue used to calculate nitrogen inputs into streams.

Tissue type	% nitrogen[b]	Reference
Conifers (general)	0.6	Triska and Sedell 1976
	0.9	Woodwell et al. 1975
Picea (spruce)	1.0	Heilman 1966
	1.4	Iversen 1974
	0.8	Watt and Heinselman 1965
	1.3	Whittaker et al. 1979
	1.4	Yamaya 1968
Alnus (alder)	3.1	Bocock 1964
	2.6	Gessner and Chauvet 1994
	3.3	Hughes et al. 1968
	4.2	Iversen 1974
	3.7	Jacobsen and Sand-Jensen 1994
	2.2	Triska and Sedell 1976
	3.4	Yamaya 1968
Rubus (bramble)	0.8	Bocock 1964
Vaccinium (blueberry)	0.6	Woodwell et al. 1975
Invertebrates	7.7	Iversen 1974
	9.0	Jacobsen and Sand-Jensen 1994
	8.6	Mattson and Scriber 1987

[a]Mean values of nonwoody plant tissue averaged across plant age, stage, locality, and environmental conditions.
[b]Based on dry mass.

water, anesthetized with tricaine methanesulfonate, their stomach contents removed, and then returned to their original habitats. Generally, 10 fish per species were sampled at each site and sampling date. Stomach contents were collected by injecting stream water into fish stomachs using a 10-mL syringe assembly (Meehan and Miller 1978); water pumped into fish stomachs forced contents out of fishes' mouths. Stomach contents and associated water, along with 95% EtOH equal in volume to that of the water, were placed into a 7 × 17 cm plastic bag; bags were labeled and returned to the laboratory where contents were identified and invertebrates counted and their body lengths measured. Invertebrate dry mass was determined with published equations as described above. I estimated lengths of partially digested prey, if actual body measurements were not possible, based on intact individuals of the same taxon that appeared similar in size. Because many prey were partially digested, this procedure apparently estimated actual prey mass ingested more accurately than would direct AFDM or volumetric estimates. It also should have eliminated bias from specimens with different amounts of schleritization (that would be digested at different rates), such as chironomid larvae verses coleopteran adults, because head capsules of even the most digested individuals were still discernible.

For contrasting consumption of TI between riparian habitats, the null hypothesis was that the quantity of TI ingested by fish was similar between the two riparian habitats. Cutthroat trout were used as a representative species because only they were common to all sites and sampling dates. I compared salmonid stomach contents between the two forest successional regimes: proportion of TI ingested (=(mg TI)/(mg TI + mg AI)) and mass of AI and TI ingested. Individual fish were subsamples (~10) and stream reaches were replicates ($n = 3$). Proportion and mass were calculated for each fish and then averaged across all fish within a study reach.

Statistical analyses

The response variable for allochthonous trap data was TI mass. Because some winged Diptera appeared to be attracted to objects placed on stream surfaces (Power 1985; Edwards and Huryn 1995), I analyzed and presented data for habitat contrasts both with and without winged Diptera contributing to input. Response variables for cutthroat trout stomach content data were TI proportion and TI and AI biomass. Statistical analyses of stomach content data were performed for July–October sampling. May–June data were insufficient for analysis. All data were analyzed with PROC-GLM (SAS Institute Inc. 1989) at $p = 0.10$ by two-way factorial (habitat × date) with repeated measure on date (df = 1,4). A p-value of 0.10 was chosen because combining low sample size with suspected high within-habitat variability would provide low statistical power. This improved power over a lower p-value. If a significant difference was detected between habitats, an additional ANOVA was performed for each sampling date, again comparing habitats, to determine which dates were significant. Unidentifiable prey, and occasional fish and soil-borne prey that generally comprised <15% of diets, were excluded from these comparisons.

Data were checked for normality, variance homogeneity, and additivity and transformed using $\log_{10}(y + 1)$ for number and mass data and $\arcsin[(y + 1)^{1/2}]$ for proportion data to meet assumptions when necessary. Transformed data were also checked to ensure that assumptions were met. Sample and treatment independence were assumed based on experimental design and protocol used. Statistical power was calculated and reported when H_0 was not rejected (Cohen 1988).

Unfortunately, increasing sample size above three was economically unfeasible. Although I presumed that low sample size ($n = 3$) would provide low statistical power, it was safer to risk low power (and potentially fail to reject null hypotheses) than to falsely conclude

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Fig. 2. Mean (A) mass and (B) nitrogen of nonwoody plant tissue (PT) and TI falling into streams ($n = 6$ for all sampling dates except $n = 4$ for early and late September and $n = 2$ for October). Error bars represent 1 SEM.

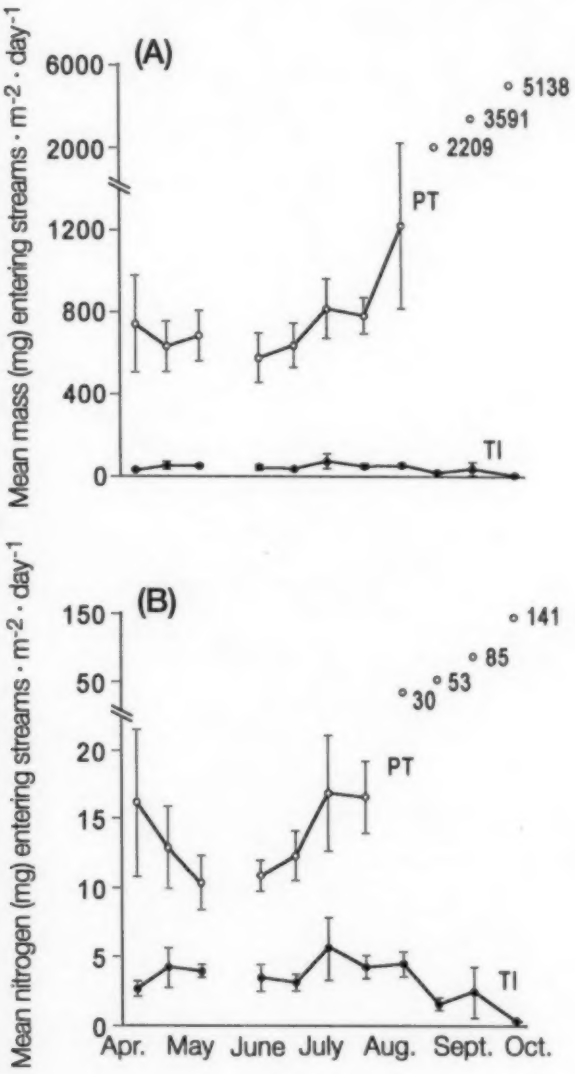
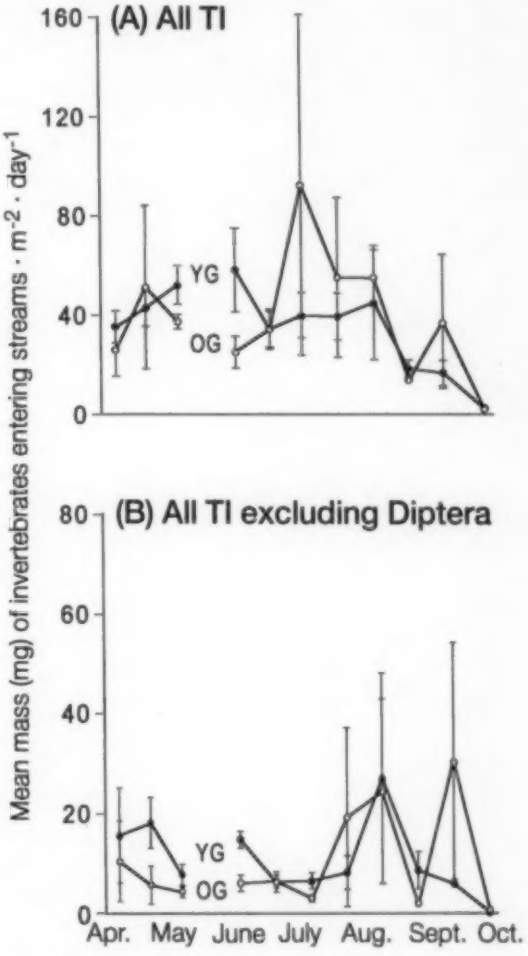


Fig. 3. Mean mass of TI captured in pan-traps in streams within old-growth (OG) and 31-year-old young-growth (YG) riparian habitats (A) including and (B) excluding winged terrestrial Diptera ($n = 3$ for all sampling dates except $n = 1$ for early September OG and October OG and YG and $n = 2$ for late September OG and YG). Error bars represent 1 SEM. Means not significantly different ($p > 0.10$).



a significant difference in a pseudoreplicated study (i.e., defining fish as experimental units (replicates) and comparing two streams or two reaches within a stream), which unfortunately, still happens with many other natural stream studies. Additionally, the p-value was set at 0.10 instead of 0.05 or 0.01 to help achieve higher statistical power.

Results

Stream inputs of terrestrial invertebrates

TI comprised a small fraction of allochthonous input relative to plant litter: up to 66 versus 5138 mg·m^{-2}·day^{-1} (Fig. 2A). Mean season-long TI input was 37 mg·m^{-2}·day^{-1}. Because of their relatively high nitrogen content, they contributed a greater fraction of total nitrogen (than of total biomass), up to 6 versus 141 mg N·m^{-2}·day^{-1}, respectively, to these streams (Fig. 2B). Mean season-long nitrogen input from TI was 3 mg·m^{-2}·day^{-1}. Their input into streams was not significantly different among habitats for analyses that included (Fig. 3A) and excluded winged terrestrial Diptera (Fig. 3B). Season-long input means including Diptera were 39 and 35 and excluding Diptera were 10 and 11 mg·m^{-2}·day^{-1} in old-growth and young-growth habitats, respectively. Diptera comprised the bulk of TI mass inputs in both habitats, followed by Coleoptera, Lepidoptera, and Araneida (Table 3).

Terrestrial invertebrates as salmonid prey

Numerically, TI comprised 30% of invertebrates in fish stomachs

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Table 3. Percent composition of TI mass captured in pan-traps.

	Riparian forest type[a]	
TI	OG	YG
Gastropoda	0.0	0.6
Chilopoda	1.3	0.0
Araneida	5.4	6.7
Collembola	0.7	1.5
Hemiptera	0.7	2.6
Coleoptera	7.2	8.0
Lepidoptera	7.8	6.4
Diptera	71.5	60.7
Hymenoptera	0.6	1.7
Other[b]	4.8	11.8

[a]OG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.

[b]Includes unidentifiable invertebrates and taxa that comprised <0.1%.

Fig. 4. Mean (A) number and (B) mass of AI and TI prey ingested by 40–180 mm fork length salmonids, averaged across all six study sites ($n = 3$ for May and June; $n = 6$ for the other months). Error bars represent 1 SEM.

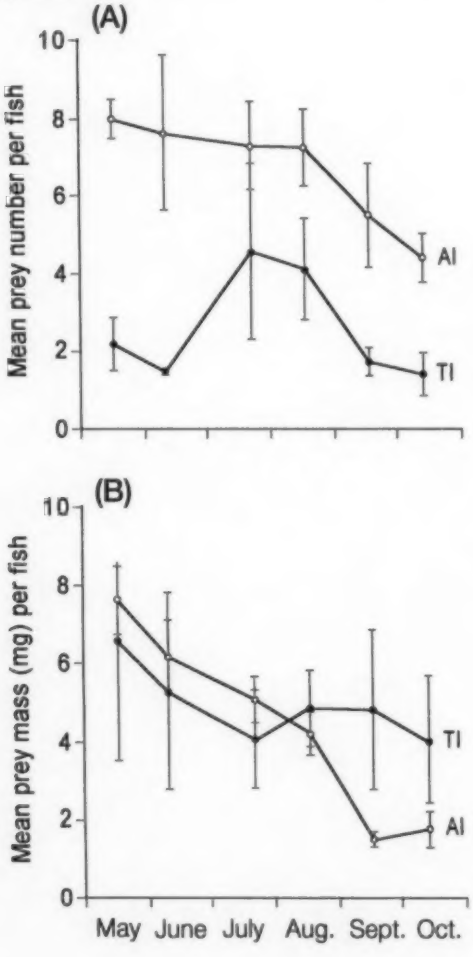
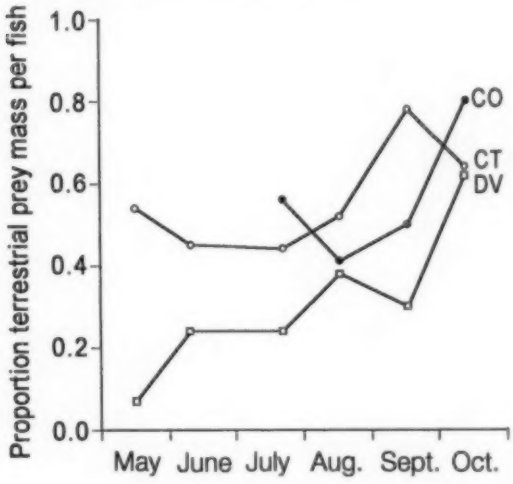


Fig. 5. Mean proportion of TI prey ingested by the three most common salmonids (coho salmon (CO), cutthroat trout (CT), and Dolly Varden (DV), 40–180 mm fork length) at all six study sites. Values = (TI mass)/(TI mass + AI mass).



(Fig. 4A) but 50% of the biomass (Fig. 4B), for combined fishes. Mass of ingested AI decreased sharply through the season whereas that for TI remained more constant (Fig. 4B). In general, TI were more abundant in fish diets later in the season (Fig. 5). Aquatic taxa (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) and Lepidoptera among TI contributed the greatest masses from individual taxa to food ingested by cutthroat trout over the season (Table 4).

Proportionally, TI were significantly more abundant in cutthroat trout diets through the season in young-growth than in old-growth systems, both numerically ($F = 8.2$, $p = 0.05$) (Fig. 6A) and gravimetrically ($F = 5.8$, $p = 0.07$) (Fig. 6B), with July the only month in which there were significant differences ($F = 10.5$, $p = 0.005$ and $F = 7.4$, $p = 0.015$, proportional number and proportional biomass, respectively). Season-long proportion means were 0.16 and 0.33 for number of terrestrial prey and 0.38 and 0.57 for terrestrial prey mass in old-growth and young-growth habitats, respectively. Although not significant, that trend appeared during all other months. These (terrestrial prey proportion) data appeared lower than what the fish actually ate (i.e., Fig. 5) because they are means of means, summed across fish and streams ($n = 3$) within habitat. (In other words, a fish that ingested one each of AI and TI was given equal "mathematical weight", for calculating means within habitat, as a fish that ingested one AI and 20 TI.) Statistical power was low ($1 - \beta < 0.30$) because of high within-stream variability and low sample size and subsequently reduced the probability of detecting habitat differences. Taxa that accounted for the most variation between habitats were Chironomidae (Fig. 7A) and Collembola (Fig. 7B). Fish ate significantly more chironomids in old-growth habitats only during July ($F = 6.3$, $p = 0.023$) (Fig. 7A). No significant habitat differences were apparent with ingested collembolans. Again, statistical power was low ($1 - \beta < 0.30$).

Aquatic invertebrate mass ingested was similar for cutthroat trout between habitats (Fig. 8A) and decreased sharply

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Table 4. Percent composition of AI and TI mass ingested by cutthroat trout.

	Riparian forest type[a]	
	OG	SG
Aquatic		
Ephemeroptera	11.6	7.3
Plecoptera	12.2	4.5
Trichoptera	15.2	18.0
Diptera	13.0	8.7
Terrestrial		
Gastropoda	0.0	2.1
Diplopoda	3.5	0.0
Chilopoda	4.4	10.7
Isopoda	1.3	0.4
Araneida	4.8	5.9
Collembola	1.1	1.4
Psocoptera	0.1	0.0
Hemiptera	1.7	4.2
Coleoptera	9.3	18.3
Lepidoptera	16.4	13.7
Diptera	0.4	0.6
Hymenoptera	2.0	2.0
Other[b]	3.0	2.2

[a]OG, old-growth riparian forest; YG, 31-year-old young-growth riparian forest.

[b]Includes unidentifiable invertebrates and taxa that comprised <0.1%.

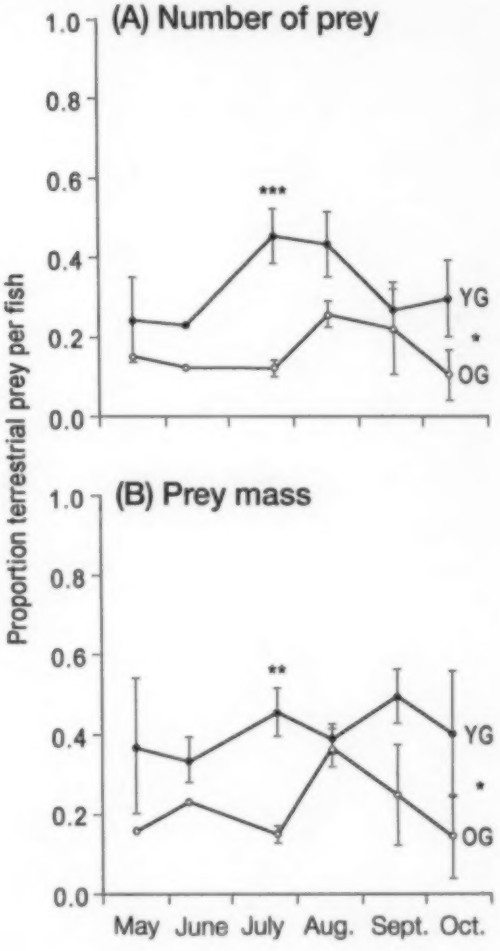
through the season for fish in both habitats; TI mass ingested was also not significant between habitats (Fig. 8B). Season-long means were 4.5 and 4.3 mg·fish^{-1} for aquatic prey ingested and 3.0 and 6.2 mg·fish^{-1} for terrestrial prey mass ingested in old-growth and young-growth habitats, respectively. As with previous analyses, power was low ($1 - \beta <$ 0.30).

Discussion

These results showed that TI were important food, as important as AI, for young coho salmon, cutthroat trout, and Dolly Varden during spring, summer, and fall in these coastal Alaska streams. The data also suggested that riparian vegetation influences associated TI that fall prey to fishes. This has several implications for riparian forest management and conservation (particularly how it relates to fisheries), stream protection and restoration, and stream ecosystem theory.

Streamside management, including activities that affect riparian vegetation, could have strong influences on stream food web productivity. The 31-year-old alder-dominated young-growth communities in this study appeared to be providing fish with more terrestrial prey (based on diet data) than the old-growth riparian forest. Two obvious characteristics of these young-growth communities, relative to the old-growth communities, were a more dense and diverse understory and a broadleaf-dominated (alder) canopy. This more diverse and possibly productive plant community may support a similarly diverse and productive TI community. Southwood (1961) noted more diverse invertebrate assemblages associated with broadleaf species. Fish in young-growth systems in this study ate a greater proportion of TI than those in old-growth systems

Fig. 6. Mean proportional (A) number and (B) mass of TI prey ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats (n = 3 for all sampling dates except n = 2 for May and June YG and n = 1 for May and June OG). Values = (TI mass)/(TI mass + AI mass). Error bars represent 1 SEM. Asterisks on the right side of the graph indicate statistically significant season-long (July–October) differences between riparian habitats and those directly above data points indicate month-specific differences (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).



during part of the summer, reflecting possibly higher TI proportions associated with denser broadleaf riparian vegetation. This possibly higher TI abundance in young-growth habitats in this study was probably attributable to the more dense broadleaf-dominated plant community and less related to this habitat simply being young-growth. Less diverse and dense understories seen with 25- to 140-year-old young-growth conifer stands (Franklin and Pechanec 1968; Alaback 1982) may sustain lower invertebrate densities and species richness.

The significant habitat difference seen with diet data did not agree with allochthonous trap data. This may have been a sampling artifact of TI traps. The traps may have been less efficient

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Fig. 7. Mean number of larval and pupal (A) Chironomidae and (B) Collembola ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats ($n = 3$ for all sampling dates except $n = 2$ for May and June YG and $n = 1$ for May and June OG). Error bars represent 1 SEM. Asterisks indicate month-specific differences between habitats (**$p < 0.05$).

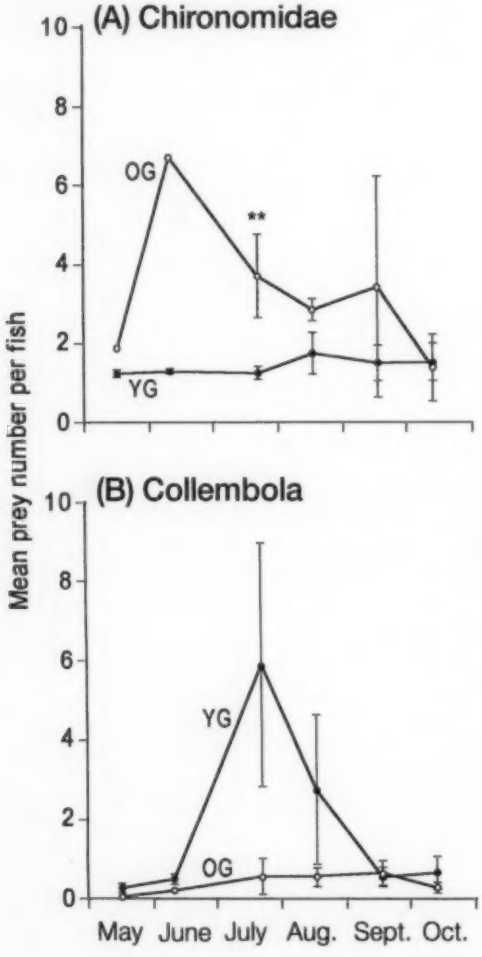
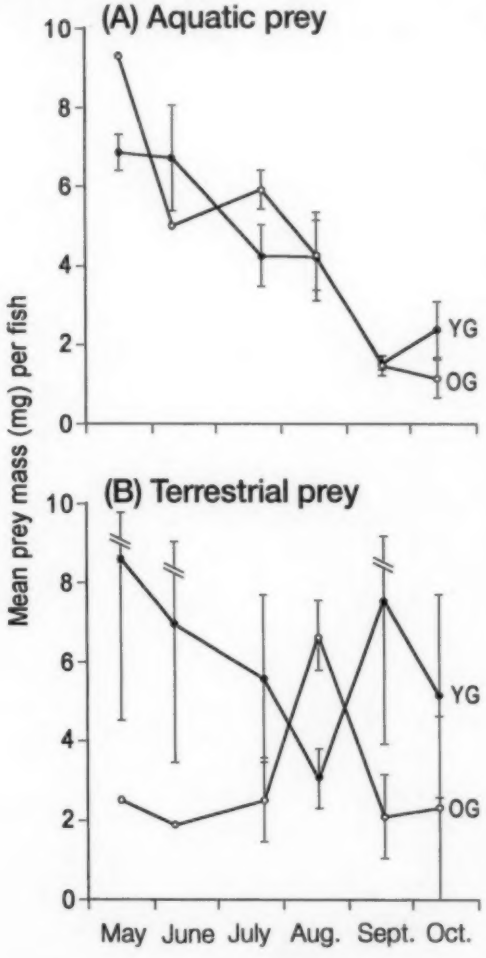


Fig. 8. Mean mass of (A) AI and (B) TI prey ingested by 40–180 mm fork length cutthroat trout, contrasting old-growth (OG) and 31-year-old young-growth (YG) habitats ($n = 3$ for all sampling dates except $n = 2$ for May and June YG and $n = 1$ for May and June OG). Error bars represent 1 SEM. Means not significantly different ($p > 0.10$).



than fish at sequestering certain prey that may have been more abundant in one habitat (e.g., strong crawlers like Coleoptera and Chilopoda may escape from the pans). Traps may also have attracted certain species, particularly winged Diptera (Southwood 1978; Power 1985; Edwards and Huryn 1995). In this study, Diptera comprised an unusually high percentage of pan-trap contents relative to fish stomach contents. However, this should not have compromised habitat comparisons, including when winged Diptera were part of the analysis, because they were about equally abundant in traps from both habitats (i.e., no habitat bias).

Difficulty with accurately measuring TI inputs into aquatic habitats may be one of the reasons quantitative inputs have not been commonly reported in the literature. Trapping methods, including pan-traps, sticky traps, and drift-capture, have their biases (Southwood 1978; Power 1985; Edwards and Huryn 1995; M.S. Wipfli, personal observation). Pan- and sticky traps may attract certain species, and nets placed in streams will not capture small invertebrates (e.g., Collembola) that pass through netting, nor do they prevent some invertebrates from crawling or flying away. Pan-traps containing a surfactant or sticky traps will help avoid these problems. Drift nets also often become clogged, leading to sample loss. Another possible reason for the paucity of these types of studies may be that aquatic and fishery biologists have traditionally not felt comfortable studying terrestrial ecology, so have ended with simply stating that terrestrial prey are important components of fishes' diets. Another explanation may be that fishery, aquatic, and terrestrial ecologists have historically worked independently. If study objectives are to achieve absolute measures of inputs, nonbiased sampling is crucial (i.e., attractant or

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repellent properties of traps are undesirable). Objectives that contrast treatments or habitats, provided that sampling techniques remain consistent across habitats, are less sensitive to errors from biased sampling techniques (i.e., both habitats receive equal bias).

Riparian management will not only affect TI, but aquatic primary and secondary production as well. Riparian vegetation is an important food resource for shredders in streams (Cummins et al. 1989) and may limit shredder communities (Richardson 1991). Broadleaf species, particularly alder, are preferred by aquatic detritivores (Iversen 1974; Friberg and Jacobsen 1994). Higher quality leaf litter increases their growth (Iversen 1974; Anderson and Grafius 1975) and abundance (Sedell et al. 1975), which may increase aquatic prey for fish. In this study, AI were particularly important as prey for fish early in the season, but their relationships to allochthonous inputs were not studied.

Another management consideration is the abundance of terrestrially derived prey for fishes when AI are sparse. Aquatic insect phenology — adult emergence during spring, summer, and fall — will temporarily reduce abundance and availability of many aquatic insects as prey for fishes and other predators. These data showed a rapid decline of AI ingested by fish beginning in May and extending through October, apparently resulting from insect emergence throughout the season. Yet, the quantity of TI ingested remained relatively stable through the season. Late summer/early fall is a critical period for fishes as they sequester lipids and increase body size, providing greater overwinter survivorship (Reimers 1963; Hunt 1969; Hartman et al. 1984). The stable riparian-derived prey supply may be crucial for salmonid survival, especially if fish are already stressed from lack of aquatic prey or suitable habitat, or other stressors.

Reduced water or substrate quality may decrease aquatic prey for fish and other predators. However, loss of all aquatic prey may mean actually only losing up to half of their prey supply if TI are as important as these data have indicated and if their populations have not been reduced. Following disturbance to a stream that substantially reduces aquatic prey abundance, terrestrial prey may help sustain aquatic predators during periods of temporary aquatic prey shortages.

These results provided new insight into the significance of riparian vegetation affecting energy flow in small streams. Aquatic food web models have traditionally often excluded TI as prey for aquatic predators (cf. Minshall 1967; Cummins 1973). This study showed that terrestrially derived prey comprised half of fishes' diets and thus were as important as aquatic prey in these stream food webs. Estimated food consumption of predators has been shown to be higher than what the benthos is believed to provide (Allan 1983; Waters 1988). Allen (1951) reported that benthic invertebrate abundance was far below that needed to support fish production in a New Zealand stream. Waters (1988, 1993) suggested that nonbenthic energy sources may help explain the Allen Paradox. Edwards and Huryn (1995) estimated that TI supported about 5% of trout production in a New Zealand stream. Dedual and Collier (1995) also indicated that TI were present but not a major constituent of trout diets in a New Zealand river whereas McLennan and MacMillan (1984) demonstrated that TI often comprised the bulk of trout diets in several New Zealand rivers. Cloe and Garman (1996) reported that terrestrial arthropod energy contributions were similar to aquatic contributions in three eastern U.S. streams, with terrestrial inputs being higher in headwater reaches. These results showed that TI comprised half of salmonid diets, suggesting that they may account for much of the presumed energy deficit implicit in the Allen Paradox. However, TI consumption in other years, streams, and ecosystems could be different.

Future stream and riparian zone restoration in southeastern Alaska will probably include managing riparian vegetation. From a salmonid fisheries productivity perspective, both habitat (Bryant 1983; Bisson et al. 1987; Dolloff 1987) and food (Chapman 1966; Mundie 1974; Mason 1976; Richardson 1993) may be important limiting factors in freshwater. Rearing habitat largely depends on in-stream CWD recruited from riparian zones (Bryant 1983; Murphy et al. 1986). Because conifers make better CWD than deciduous trees along the Pacific Northwest coast — they grow larger and decompose more slowly (Harmon et al. 1986) — riparian management may involve selectively thinning less desirable species to promote growth and volume of desirable species (conifers). Thinning the canopy and understory will have dramatic effects on subsequent plant community dynamics: species composition, densities, succession, etc. This should have a dramatic effect on riparian and stream food web productivity, including that of invertebrates. Changes in riparian vegetation will directly influence associated terrestrial arthropods and will affect AI that process allochthonous material. Managers need to consider all possible effects of riparian management activities in this region and other parts of the world, including those on food resources for predators. Vegetation management will influence stream/riparian trophic productivity, thereby affecting fisheries and wildlife.

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Egg production rates of *Calanus finmarchicus* in the Northwest Atlantic (Labrador Sea)

J. Cabal, L.R. Harris, and E.J.H. Head

Abstract: Egg production rates and population characteristics of *Calanus finmarchicus* were examined in the Labrador Sea during the spring of 1994. Several experiments were conducted in order to compare egg production rates and clutch size using different types of container and in the presence and absence of food. In one series of experiments, individual females were incubated either in petri dishes or in polycarbonate bottles (80 mL) in filtered seawater. In these experiments, clutch sizes and egg production rates were not significantly different. In a second series of experiments, groups of 20 females were placed in containers under three sets of conditions: in the presence of food and with a screen to separate copepods from their eggs (FSCREEN), in the presence of food without a screen (FOOD), and in filtered seawater without a screen (FSW). Average egg production rates of female *C. finmarchicus* were significantly higher in the FSCREEN treatments than in either of the other two. In these experiments, egg production rates were not obviously related to ingestion rates, and these in vitro observations together with observations of in situ conditions suggest that stored reserves may have been used to fuel, or supplement, reproduction in *C. finmarchicus* in this area.

Résumé : Les taux de production d'oeufs et les caractéristiques de la population de *Calanus finmarchicus* ont été examinés en mer du Labrador au printemps 1994. Plusieurs expériences ont été réalisées pour comparer les taux de production d'oeufs et la taille des pontes en utilisant différents types de contenants ainsi qu'en présence et en absence d'aliments. Dans une série d'expériences, des femelles individuelles ont été incubées soit dans des boîtes de Petri ou dans des bouteilles de polycarbonate (80 mL) dans de l'eau de mer filtrée. Dans ces expériences, la taille des pontes et le taux de production d'oeufs n'étaient pas différents de manière statistiquement significative. Dans une seconde série d'expériences, des groupes de 20 femelles ont été placés dans des contenants dans trois ensembles de conditions : présence d'aliments et présence d'une grille pour séparer les copépodes de leurs oeufs (ALIGRILLE), présence d'aliments et absence de grille (ALI) et eau de mer filtrée et absence de grille (EMF). Le taux de production moyen d'oeufs des femelles de *C. finmarchicus* était significativement plus élevé dans le cas du traitement ALIGRILLE que dans les deux autres traitements. Dans ces expériences, les taux de production d'oeufs n'étaient pas liés de manière évidente aux taux d'ingestion, et ces observations in vitro, combinées aux observations dans les conditions in situ, indiquent que les réserves stockées peuvent avoir été utilisées pour alimenter la reproduction de *C. finmarchicus* dans cette région, ou la renforcer.
[Traduit par la Rédaction]

Introduction

Egg production rates have frequently been used to study production processes and recruitment rates in populations of planktonic copepods (Dagg 1977; Checkley 1980; Runge 1984, 1985*b*; Peterson and Bellantoni 1987; Hirche 1989, 1990; Plourde and Runge 1993). Estimates of the egg production rates of *Calanus finmarchicus* are important in the Labrador Sea because this species constitutes over 60% of the biomass of zooplankton in the Northwest Atlantic Ocean (Tremblay and Roff 1982), and its eggs and nauplii can constitute a substantial proportion of the diet of many species of fish of commercial interest (Kane 1984; Runge 1988; Runge and De Lafontaine 1996). Reports of egg production rates of *C. finmarchicus* in the literature are variable (e.g., Runge 1985*a*; Hirche 1990; Diel and Tande 1992) because they can be affected by a variety of biotic (e.g., food concentration, cannibalism) and abiotic (e.g., temperature) factors. Moreover, because a variety of experimental techniques have been used (Laabir et al. 1995), comparisons of egg production rates obtained by different authors may be questionable.

Several incubation methods have been used to estimate egg production rates (Runge 1985*a*, 1985*b*; Laabir et al. 1995). Egg production by individual females has been investigated in petri dishes or small-volume bottles (Runge 1984, 1985*a*), while egg production rates for groups of females have been studied in vessels with or without a screen (a mesh sieve fixed near the bottom of the incubation vessel) and in the presence or absence of food (Runge 1985*a*; Diel and Tande 1992; Plourde and Runge 1993). Incubations with individual females have the advantage that they allow measurements of spawning frequency and the number of eggs in a spawning event (clutch size).

Several field studies of *C. finmarchicus* have suggested that reproduction does not begin before the spring development of phytoplankton (Fransz 1975; Runge 1985*a*; Diel and Tande 1992; Plourde and Runge 1993), and experimental studies have shown a curvilinear relationship between *C. finmarchicus* egg production rate and food supply, with females stopping egg

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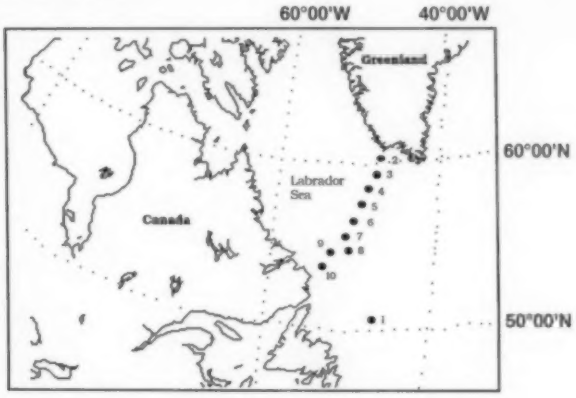
Fig. 1. Locations of the sampling stations in the Northwest Atlanctic Ocean.



production in the absence of food (Plourde and Runge 1993). However, there are also reports of spawning occurring before the onset of the spring bloom (Marshall and Orr 1952; Melle and Skjoldal 1989; Diel and Tande 1992), and it has been proposed that lipid reserves may be sufficient to begin egg production without an external food supply (Gatten et al. 1979).

The aim of this work was to compare estimates of egg production rates and clutch sizes of *C. finmarchicus* using a variety of containers and food concentrations. We have also compared these results with hydrographic and biological conditions in the subarctic Labrador Sea in order to examine the relationship between reproduction of *C. finmarchicus* and the state of the spring bloom.

Methods

Sampling procedures

The field work was carried out aboard the CSS *Hudson* between May 24 and June 10, 1994. Observations were made at 10 stations, which were sampled during daylight hours. Nine of the stations were along a transect between the Greenland coast and the edge of the ice-pack off the Labrador coast and the tenth was further south on the Newfoundland Shelf (Fig. 1). At each station, temperature and salinity profiles were obtained with a Seabird CTD. Samples of seawater for the determination of chlorophyll (filtered onto glass fiber filters GF/F) and nutrients were collected with a pump at 10-m depth intervals within the upper 100 m of the water column. Mesozooplankton samples were collected using ring nets with two different-sized meshes (80 and 200 μm). The nets were towed vertically between 100 m and the surface. Samples collected with the 80-μm net were preserved in formalin (2%). Samples collected using the 200-μm net were either preserved in formalin (2%) for systematic studies or immediately diluted with surface seawater for experimental use.

Egg production rates were measured for *C. finmarchicus* females that had been sorted using a dissecting microscope. To examine the vertical distribution of *C. finmarchicus* eggs and females, 100-L samples of seawater were collected at depths of 3, 10, 20, 30, 40, 50, 75, and 100 m at stations 4 and 8 using a biological pump fitted with a Seabird CTD probe and a submersible fluorometer. The seawater was screened through a 100-μm mesh, and the females and eggs collected on the screen were preserved in formalin (2%).

Seawater samples, to be used as food in the experiments, were collected by pump at the depth of the chlorophyll maximum. The seawater was stored, in the dark, in polyethylene carboys in a deck incubator. Seawater from the same depth was used to make filtered seawater (<0.2 μm) for the incubations in which food was absent.

Table 1. Summary of conditions in situ and experimental incubations. Chlorophyll (Chl) is the average of the initial concentrations in all of the bottles that contained food in each experiment (see text for explanation).

Date	Station	Surface temp. (°C)	Chl at the Chl max. ($\mu g \cdot L^{-1}$)	Chl in the experiments ($\mu g \cdot L^{-1}$)	Type of experiments
May 27	1	0.31	11.20	8.60±0.47	2
May 29	4	3.59	1.13	0.67±0.05	1,2
May 31	3	3.61	1.76	1.34±0.04	2
June 1	5	3.58	1.08	0.81±0.09	1,2
June 2	6	3.57	1.32	0.90±0.08	2
June 3	7	0.65	2.79	2.48±0.10	2
June 4	8	0.90	2.96	1.59±0.19	1,2
June 5	9	−1.05	14.05	12.00±0.58	2
June 6	10	0.53	11.96	11.96±0.16	2

Experimental procedures

Type 1 experiments: egg production rates for individual females

Egg production rates and clutch size of *C. finmarchicus* were estimated in two types of vessels containing similar volumes of filtered seawater (i.e., without food). At three stations, 20 females were placed individually in 10 plastic petri dishes and in 10 polycarbonate bottles, each of which contained 80 mL of filtered seawater (Table 1). The level of cannibalism is supposedly reduced in petri dishes (Runge 1985*a*). The samples were incubated in the dark in a refrigerator at 1–3°C which was close to the in situ surface temperature (±1°). Incubations were for 72 h, with the animals being transferred every 24 h to new incubation vessels and the eggs being collected on a 28-μm sieve and preserved in buffered formalin (2%). Clutch sizes of less than 5 eggs·animal^{-1} were not included in estimates of mean clutch size and egg production rate (Marshall and Orr 1955; Runge 1984).

Type 2 experiments: feeding and fecundity experiments

These experiments were designed to compare egg production rates among different types of containers in the presence or absence of food and to compare these results with the experiments described above. Experiments of this type were carried out at nine stations (Table 1). Fifteen to 20 females were put into each of six containers. Two of them consisted of 1-L Plexiglas cylinders suspended in 2-L jars (FSCREEN treatment). The cylinders had 300-μm meshes on the bottom to prevent cannibalism of the eggs. The 2-L jars contained water from the depth of the chlorophyll maximum, which had been screened through a 100-μm mesh. The other four containers were 1-L polycarbonate bottles, two of them containing screened seawater (100 μm) from the chlorophyll maximum depth, as in the FSCREEN treatments (FOOD treatment), and two containing filtered (<0.2 μm) seawater (FSW treatment). Another two 1-L polycarbonate bottles were filled with screened (100 μm) seawater from the depth of the chlorophyll maximum without copepods to serve as controls (CONTROL) for calculating ingestion and filtration rates.

All containers were held for 72 h in an incubator through which surface seawater was flowing. The temperature of the water in the incubator was between 2 and 4°C and was generally within 2°C of the temperature of in situ surface seawater. Every 24 h, eggs were screened off, using a 28-μm sieve, and preserved in buffered formalin (2%) for subsequent examination in the laboratory. The animals were then transferred to new incubation vessels with fresh filtered seawater or food. Water subsamples were filtered (glass fiber filters GF/F) at the start and end of each incubation period to estimate chlorophyll

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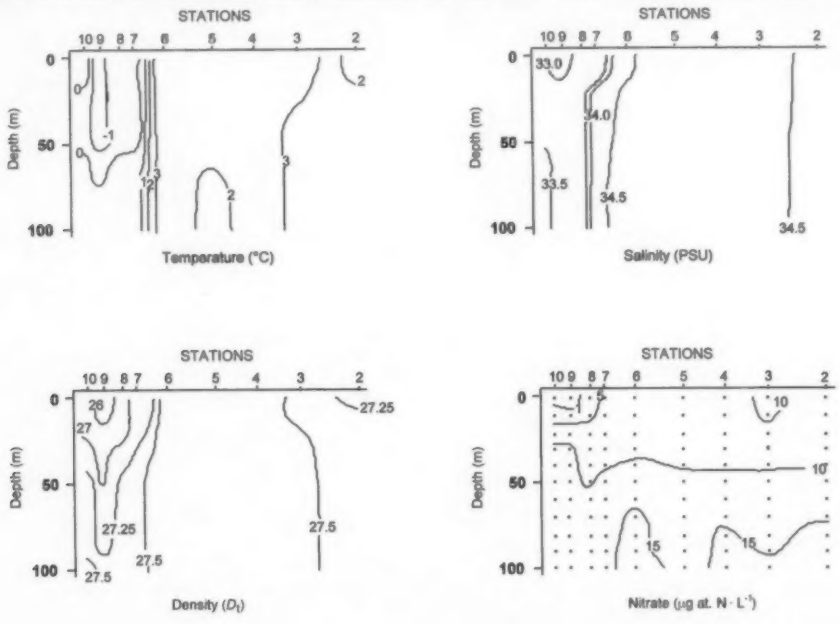
Fig. 2. Vertical distribution of temperature, salinity, density, and nitrate along the transect between Labrador and Greenland.



concentrations which were used to calculate filtration and ingestion rates, after correcting for differences between CONTROL and experimental bottles. Chlorophyll concentrations were measured on extracts of filters in 90% acetone using a Turner Designs fluorometer (Holm Hansen et al. 1965). All the seawater to be used in each experiment was collected at the same time and at the same station as the animals. It was screened (100 µm) immediately before each incubation was set up. Experimental daily egg production rates were calculated by dividing the total number of eggs found in a sample by the number of females in the container after normalizing the time interval to 1 day.

In situ egg production rates of *C. finmarchicus* females were also estimated using the "egg ratio" method (Edmondson et al. 1962) for which the assumption was made that the eggs did not sink out of the top 100 m before hatching. The females and eggs in the preserved samples from the 80-µm vertical net tows were counted, and the egg production rates were estimated using the expression $F = N_e/(D_t \cdot N_f)$ where F is the daily egg production rate (eggs per female per day), N_e and N_f are estimates of abundances of eggs and female copepods (number per square metre), respectively, in the water column, and D_t is the hatching time (days) of the eggs at the ambient temperature (T, degrees Celsius). D_t was estimated from equation $D_t = 27.7(T + 4.57)^{-1.10}$ derived from hatching time of *C. finmarchicus* eggs (Corkett 1972). T was calculated as the average temperature over the 100 m of water column. We chose this formula because the results coincided with some experimental observations of egg hatching times that were made during the cruise at 3°C.

The stage of gonad maturation was assessed in preserved adult females. Between 40 and 50 females from each station were stained with a solution of fast green (Batchelder 1986). The classification of oocyte maturity stages was from the descriptions provided by Runge (1987) and Tourangeau and Runge (1991). Copepods with only previtellogenic and early vitellogenic oocytes (stages 1–3) were considered to be in a nonspawning state. Females in stages 4–7 were classified as actively spawning because of the presence of oocytes undergoing secondary vitellogenesis (Runge 1987).

Carbon and nitrogen contents of eggs and female *C. finmarchicus* were measured with a Perkin Elmer 2400 CHN elemental analyzer to estimate productivity (P/B ratio) of females. Eggs were picked by pipette and washed several times in filtered seawater before being placed on precombusted GF/F filters. Several samples ($n = 9$) with 100–500 eggs were analyzed. Eggs were collected in experiments done in parallel with those described here, but with higher numbers of females. Females (for carbon and nitrogen analysis) were picked individually or in groups of 20 before and after experimental incubation. Samples were stored at –20°C for 3 weeks prior to analysis.

Statistical analysis

Raw data were transformed, when necessary, to achieve statistical assumptions of linearity, normality (Kolmogorov–Smirnov test), and homogeneity of variances (Cochran's test) which are required for most statistical analyses (Sokal and Rohlf 1981). Group means were compared with the Ryan–Einot–Gabriel Welsch multiple F-test (REGWF test) in ANOVA performed with stations and treatment as factors. Stations were considered to have a random effect and treatment a fixed effect (Zar 1984). Egg production rates between treatments were compared with a t-test and probability level was adjusted for multiple comparison with the sequential Bonferroni correction (Rice 1989). Pearson's correlation coefficients were used to describe the relationship between pairs of variables.

Results

Hydrography, phytoplankton, and zooplankton distributions

There were pronounced variations in the vertical structure of the water column along the transect (Fig. 2). In the central Labrador Sea, the density of the water column was homogeneous whereas the density gradient was steep at stations near the Labrador coast. The lowest temperatures (below –1°C) and salinities occurred near the pack-ice that covered the shelf off the Labrador coast, and between these and the central area of the Labrador Sea, there was a hydrographic front.

Maximum concentrations of chlorophyll were at depths

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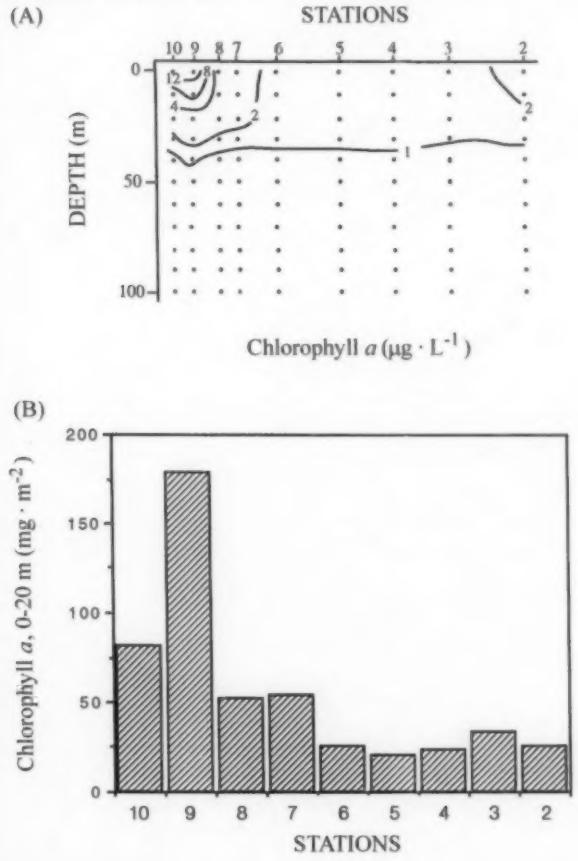
Fig. 3. (A) Vertical distribution of chlorophyll and (B) integrated concentration of chlorophyll (0–20 m) along the transect between Labrador and Greenland.



between the surface and 30 m at all stations (Fig. 3A). The highest concentration of chlorophyll (14 $\mu g \cdot L^{-1}$) occurred at station 10 near the coast of Labrador, where meltwater had induced stratification, which had led to intense algal production and depletion of surface nitrate (Fig. 2). Close to the pack-ice the surface chlorophyll distribution was patchy (J. Cabal, personal observation). Chlorophyll concentrations integrated over the upper 20 m of the water column were higher than 20 $mg \cdot m^{-2}$ throughout the transect, and the highest concentrations were found at stations near the Labrador coast (Fig. 3B).

At all stations the numerically dominant zooplankton (>200 μm) were copepods (average 86.8%, SD 5.8). *Calanus finmarchicus* was the most abundant species at most of the stations, except near the Labrador coast at stations 9 and 10 (Fig. 4A). The other relatively abundant species were *Calanus glacialis, Calanus hyperboreus*, and *Oithona* spp., the latter two becoming more common near the Labrador coast.

The stage composition of *C. finmarchicus* populations varied along the transect. In the area nearest Labrador, females were most abundant (>50%), and the rest of the population was composed of stages CV and CIV. For the stations in the central Labrador Sea and near Greenland, females accounted for 10–40% of the population and stages CI, CII, and CIII were

Fig. 4. (A) Abundance of mesozooplankton and *C. finmarchicus* and (B) stage composition of *C. finmarchicus* along the transect between Labrador and Greenland.

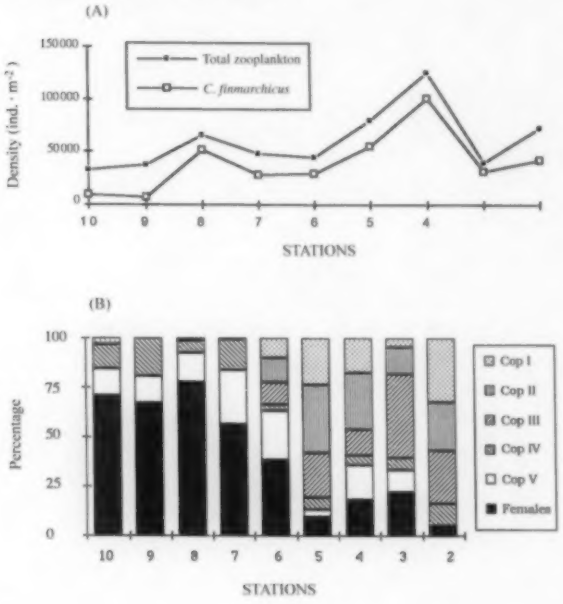
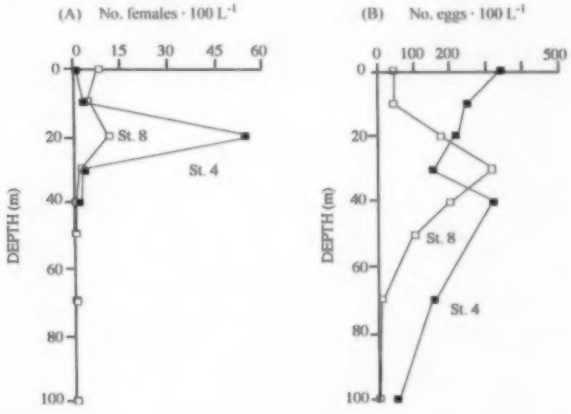


Fig. 5. Vertical distribution of (A) *C. finmarchicus* females and (B) eggs at stations 4 and 8.



more abundant than females (Fig. 4B). Female *C. finmarchicus* at stations 4 and 8 were restricted to the upper 40–50 m of the water column during the day, and their maximum abundances were at 20 m (Fig. 5A). Copepod eggs were more broadly dispersed throughout the water column, with maximum abundances at depths of more than 20 m (Fig. 5B).

Experimental egg production rates

Type 1 experiments: egg production rates for individual females

The distribution of clutch sizes was similar for the two different types of container (Fig. 6). The largest clutch size was 129

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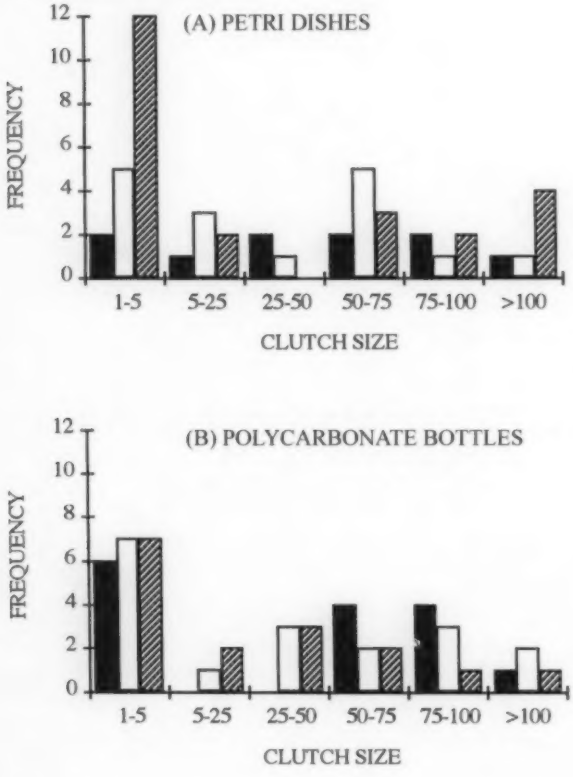
Fig. 6. Clutch size (eggs·female^{-1}) distributions at stations 4 (solid bars), 5 (open bars), and 8 (hatched bars) in the type 1 experiments. The results are from each of the 3 days of incubation and clutch sizes of 0 are not included.



eggs for a female in a petri dish, but this was only slightly higher than the highest value found in a bottle (105). Over the 3 days of incubation, the egg production rates for females incubated in petri dishes were not significantly different from those for females incubated in polycarbonate bottles containing the same volume of filtered seawater (Table 2). Egg production rates were higher on the first day of incubation than on the second and third days (Table 3).

Type 2 experiments: feeding and fecundity experiments

Results obtained for the nine experiments of this type (Table 4) showed a significant treatment versus station interaction for the 3-day averages (Table 5). The trends in the response of *C. finmarchicus* females did not vary in parallel, although both treatment and station effects alone were significant. Because their interaction was significant, however, the effect of treatment was tested separately for the different sampling stations (e.g., Gill 1978; Werner 1991). Separate *t*-tests (results not shown) for the 3-day average egg production rate versus treatment for each station indicated that the treatment effect was significant for five of the stations (sequential Bonferroni correction for multiple test applied, Rice 1989). When separate ANOVAs were performed for each day of incubation for all stations and then on the second and third days, the effects of station and the interaction of station versus treatment were not

Table 2. ANOVA for the effect of treatment (polycarbonate bottle or petri dish) on egg production rate of *C. finmarchicus* females in the individual egg production rates (type 1 experiments).

Source of variation	Sum of squares	df	F	$p > F$
Average for 3 days of incubation				
Station	4928.00	2	10.22	0.001
Treatment	488.53	1	2.02	0.1
Station × treatment	308.29	2	0.64	0.5
Residual	8915.92	37		

significant, but the effect of the treatment was still significant (Table 5).

Average egg production rates for females *C. finmarchicus* calculated over the 3-day incubation periods were 9.06 eggs·female^{-1}·day^{-1} in FOOD treatments and 7.77 eggs·female^{-1}·day^{-1} in FSW treatments, while in the FSCREEN treatments, the average egg production rate was 18.12 eggs·female^{-1}·day^{-1} and this difference was significant (REGWF, $p = 0.05$).

Egg production rates for the first day of incubation were higher in the FSCREEN treatment than in the other two treatments, except at stations 1 and 10, where they were similar in all three treatments. Chlorophyll concentrations were high at these two stations (>8 μg·L^{-1}), but at station 9, where the experimental chlorophyll concentration was 12 μg·L^{-1}, this pattern did not occur. The in situ history of the animal (pre- versus during spring bloom) made little difference to egg production rates. Also, daily egg production rates tended to decrease over the 3 days of incubation in all three types of treatment (FSCREEN, FOOD, and FSW), even though new food was added on the second and third days in the FSCREEN and FOOD treatments.

Initial chlorophyll concentrations in the incubations varied between 0.7 and 12 μg·L^{-1}, although experimental temperatures varied little (Table 1). Average filtration and ingestion rates were 1.26 ± 0.61 mL·female^{-1}·h^{-1} and 7.9 ± 9.30 ng Chl·female^{-1}·h^{-1} in the FOOD treatments and 0.72 ± 0.31 mL·female^{-1}·h^{-1} and 4.17 ± 4.76 ng Chl·female^{-1}·h^{-1} in the FSCREEN treatments. Egg production rates in the FSCREEN treatments were not correlated with the experimental concentrations of chlorophyll ($r = 0.0435$, $p = 0.764$) or with experimental ingestion rates ($r = 0.0035$, $p = 0.981$). In fact, average egg production rates were not very different in experiments with low versus high concentrations of chlorophyll. They were, however, very variable and the highest rates were generally only attained in experiments with chlorophyll concentrations >2.5 μg·L^{-1} (Fig. 7A).

Differences in egg production rates between the FSCREEN and FOOD treatments can be used to estimate cannibalism, if we assume that cannibalism occurred in the FOOD but not the FSCREEN treatments. Using this assumption, rates of cannibalism were found to vary between 0 and 28 eggs·female^{-1}·day^{-1} (average 10). Cannibalism was negatively correlated with the concentration of chlorophyll in the FOOD treatment (Pearson $r = -0.4159$, $p = 0.003$), but not with ingestion rate ($r = -0.1960$, $p = 0.172$). Stepwise multiple regression analysis, however, showed that both the concentration of food and ingestion rate contributed to the variation in egg production rate in the FOOD treatment (Table 6). Thus, it appears that

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Table 3. Spawning frequency (Fr), clutch size (CS), and egg production rates (EPR) of female *C. finmarchicus* in type 1 experiments over the first, second, and third 24-h periods, and daily average values for the entire 72-h incubation.

	0–24 h			24–48 h			48–72 h			Average		
	Fr	CS	EPR	Fr	CS	EPR	Fr	CS	EPR	Fr	CS	EPR
Station 4												
Petri dish	0.4	93.3	27.7	0.3	48.4	14.4	0	0	0	0.5	58.0	29.2
		(13.6)	(1.7)		(10.4)	(3.2)					(18.2)	(3.8)
Bottle	0.6	74.2	32.3	0.1	50.0	5.6	0.2	77.5	15.5	0.8	46.8	37.4
		(18.9)	(5.1)			(2.2)		(1.5)	(3.5)		(16.6)	(2.7)
Station 5												
Petri dish	0.2	107.0	21.0	0.3	67.3	20.1	0.4	46.2	13.8	0.7	24.7	17.3
		(22.0)	(4.1)		(7.1)	(3.8)		(19.7)	(3.1)		(10.2)	(2.3)
Bottle	0.5	55.8	25.7	0.1	60.2	6.0	0.4	42.5	17.0	0.7	22.1	15.5
		(4.5)	(5.1)			(2.3)		(9.3)	(3.2)		(6.3)	(2.1)
Station 8												
Petri dish	0.8	62.3	49.8	0	0	0	0.1	83.0	8.3	0.8	35.4	28.3
		(17.2)	(3.2)						(2.8)		(13.5)	(2.4)
Bottle	0.7	51.8	34.5	0	0	0	0.3	41.3	12.4	0.7	21.3	14.9
		(12.4)	(3.4)					(4.9)	(2.9)		(7.8)	(2.1)

Note: Rates were calculated from daily frequency of spawning and clutch size by assuming a binomial distribution for spawning frequency. SD is given in parentheses.

increases in ingestion rate lead to decreases in egg production rate, perhaps because of an increase in the number of eggs eaten, whereas increases in the concentration of food lead females to eat fewer eggs. A comparison of the numbers of eggs produced in the FSCREEN treatments with those produced in the FSW treatments suggests that rates of cannibalism were even higher in the absence of food (by about 57%).

There were three stations at which type 1 and type 2 experiments were run in parallel: stations 4, 5, and 8. Rates of egg production by *C. finmarchicus* females in the FSCREEN treatments were similar to those observed for individual females in the low-volume petri dishes and bottles over the course of the first day at all three stations and over all 3 days at stations 5 and 8. Egg production rates in the FSW and FOOD treatments, however, were lower (Tables 3 and 4).

Egg production rates versus in situ conditions

Egg production rates were low (5 eggs·female^{-1}·day^{-1}) in experiments with *C. finmarchicus* females from stations near the coast of Greenland. At stations in the centre of the transect and near the Labrador coast, egg production rates in incubations were similar (around 20 eggs·female^{-1}·day^{-1}) and the highest values were found at stations 5, 6, and 8 (Fig. 7B). Egg production rates were not correlated with integrated chlorophyll concentrations in the water column ($r = 0.196$, $p = 0.613$).

In situ egg production rates, estimated using the egg ratio method, were not the same as those seen in the incubations (Figs. 7B and 7C). In situ rates of about 60 eggs·female^{-1}·day^{-1} were calculated for coastal stations and at station 5. For the other stations, in situ rates were apparently less than 10 eggs·female^{-1}·day^{-1} (Fig. 7C). By contrast, the gonad maturation index for *C. finmarchicus* females from preserved samples was similar at all stations: more than 90% of females were in stages 5, 6, and 7, and only at stations 9 and 10 was this proportion lower, at around 80–85% (Fig. 8).

Carbon and nitrogen egg production budgets

Analysis of the elemental composition of eggs gave a carbon content of 0.245 ± 0.05 µg and a nitrogen content of 0.04 ± 0.01 µg·egg^{-1}. Females contained 164.29 ± 18.91 µg C and 37.4 ± 5.26 µg N·individual^{-1}. Thus, the maximum egg production rate in the FSCREEN treatment of 37.84 eggs·female^{-1}·day^{-1} and the average rate of 20.69 eggs·female^{-1}·day^{-1} were equivalent to a maximum of 9.27 µg C·female^{-1}·day^{-1} and an average of 5.07 µg C·female^{-1}·day^{-1}. Egg production was therefore equivalent to a maximum of 5.64% and an average of 3.08% of body carbon per day and to a maximum of 4.04% and an average of 2.21% of body nitrogen per day.

Discussion

Comparison of egg production rates in incubation experiments

One of the problems in obtaining appropiate estimates of in situ egg production rates from incubation experiments is the variability in behaviour among individual females. The rate of egg production and number of eggs produced are determined by the rates of processes involved in oogenesis and also by behavioural control over the release rate once the ova have matured (Runge 1984). In addition to this natural variability, however, we also observed variability in the measured rates when we used different methods of incubation.

For the three stations at which type 1 and type 2 experiments were run in parallel, egg production rates in the type 1 experiments were similar to those obtained in the FSCREEN treatments from the type 2 experiments. It is probable that the rates in the FSCREEN treatements were higher than in the FSW or FOOD treatments because the screen limited cannibalistic feeding by the females. In the type 1 experiments, cannibalism was also reduced, partly perhaps because densities of females were lower (1 female versus >2 females·80 mL^{-1}), but also partly because the eggs probably sank and became unavailable to the copepods, either because of the size and shape of the petri dishes or because the 80-mL bottles were not well agitated during the incubation period. In the type 1 experiments, mean estimates of egg production rates of

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Table 4. Egg production rates (average ± SD) of female *C. finmarchicus* in the feeding and fecundity experiments (type 2 experiments) over the first, second, and third 24-h periods and average daily rates for the entire 72-h incubation.

	0–24 h	24–48 h	48–72 h	Average
Station 1				
FSW	31±1.85	7±0.50	4±1.05	14±12.13
FOOD	29±6.24	13±2.01	20±3.52	21±6.39
FSCREEN	30±0.03	21±5.98	9±3.61	20±8.60
Station 4				
FSW	10±1.33	3±1.10	1±1.27	5±3.67
FOOD	1±0.58	0.3±0.07	0.02±0.02	0.5±0.43
FSCREEN	19±2.20	12±4.75	5±1.03	12±5.74
Station 3				
FSW	1.5±1.5			
FOOD	2±0.47			
FSCREEN	5±0.72			
Station 5				
FSW	13±0.30	5±1.43	1.5±0.24	8±3.67
FOOD	12±2.50	9±0.23	8±1.12	8±3.00
FSCREEN	27±2.30	17±3.14	13±6.60	19±5.74
Station 6				
FSW	6±3.35	3±0.85	5±0.93	5±1.25
FOOD	14±1.89	7±3.93	0.2±0.04	8±7.33
FSCREEN	29±4.35	16±0.98	14±8.64	18±4.26
Station 7				
FSW	8±0.26	11±2.28	2±0.31	7±3.67
FOOD	9±4.41	5±0.59	4±0.78	6±2.21
FSCREEN	16±5.69	6±0.40	14±7.27	12±4.53
Station 8				
FSW	28±1.01	12±2.84	4±1.81	15±9.91
FOOD	14±0.07	5±4.69	2±0.91	7±5.01
FSCREEN	37±0.38	23±11.60	21±4.68	27±7.41
Station 9				
FSW	12±4.95	4±3.71	0.48±0.01	6±5.03
FOOD	7±6.59	3.5±0.80	8±3.31	6±1.91
FSCREEN	17±2.44	12±4.66	20±1.18	16±3.02
Station 10				
FSW	20±0.64	0.8±0.57	2±0.81	8±8.85
FOOD	23±0.03	6±2.97	11±7.21	13±7.16
FSCREEN	20±1.95	20±6.57	15±6.83	19±2.23

individual females showed high standard deviations, and to reduce this, a larger number of replicates would have been required. Marshall and Orr (1955) have reported estimates of fecundity of *C. finmarchicus* using 100 replicates. Doing this many replicates with individual females is time-consuming, although this is the only way to measure clutch sizes. Using bottles with screens is more convenient, and probably gives realistic egg production rates, although our rates might have been still higher if we had used lower densities of females (to reduce cannibalism still further) and if we could have devised an incubator in which the food, which tended to sink through the screen, could have been maintained in suspension, while the eggs were still able to settle out.

Concentrations of phytoplankton at stations along the transect were equal to or higher than the concentration that has been found by several authors to sustain maximum rates of egg production by *Calanus* spp. Indeed, our incubation experiments suggested that at high concentrations of chlorophyll, egg production rates by females may have been maximal (Fig. 7A). Plourde and Runge (1993) found a similar effect and suggested that the critical concentration for the maximum egg production rate was about 25 mg Chl·m^{-2} (in a 20-m water column). In this study, concentrations of chlorophyll in the upper 20 m were generally greater than this, and this was true even though the spring bloom did not seem to have started at most stations.

Table 5. ANOVA for the effect of treatment on egg production rate of *Calanus finmarchicus* females in type 2 experiments.

Source of variation	Sum of squares	df	*F*	$p > F$
Average for 3 days of incubation				
Station	711.05	7	10.82	0.005
Treatment	1017.24	2	54.22	0.005
Station × treatment	375.00	14	2.85	0.01
Residual	225.32	24		
Day 1				
Station	2223.68	7	22.04	0.001
Treatment	988.54	2	6.84	0.005
Station × treatment	1010.72	14	5.01	0.001
Residual	345.89	24		
Day 2				
Station	406.19	7	1.97	0.1
Treatment	1092.65	2	15.85	0.001
Station × treatment	482.00	14	1.17	0.1
Residual	704.00	24		
Day 3				
Station	311.93	7	1.57	0.1
Treatment	1075.86	2	10.17	0.005
Station × treatment	740.38	14	1.86	0.1
Residual	682.15	24		

In the type 2 experiments where food concentrations were very low, there was generally a decrease in egg production rate over the 3 days of the incubation (Table 4, stations 4–8). This might have been because ingestion of some food was in fact required to maintain the initially high egg production rates. A decrease in egg production rate was also seen in the petri dishes (type 1 experiments, Table 3) where food was absent, and even in some of the FOOD and FSCREEN treatments in the type 2 experiments where food was abundant (Table 4). Overall, in the treatments where cannibalism was limited, it seems that egg production rates of females on day 1 of each experiment (type 1 or type 2) were probably reflecting previous in situ feeding history and that decreases in egg production rates on days 2 and 3 were an experimental effect due to lack of food or insufficient ingestion of food. Marshall and Orr (1952) also reported that the spawning of *C. finmarchicus* varied with the level of food and stopped after some time without food.

The egg production rates of *C. finmarchicus* estimated in our experiments were similar to values obtained by other authors. Hirche (1990) observed egg production rates of 19.94 ± 5.7 eggs·female^{-1}·day^{-1} in polar waters at temperature of 0°C. Diel and Tande (1992) reported a mean daily egg production during the "start" phase of egg production of 10 eggs·female^{-1}·day^{-1}, followed by an increase to 23 eggs·female^{-1}·day^{-1}. Runge (1985*a*) observed egg production rates of 26 eggs·female^{-1}·day^{-1} at 5.3°C in waters off Nova Scotia.

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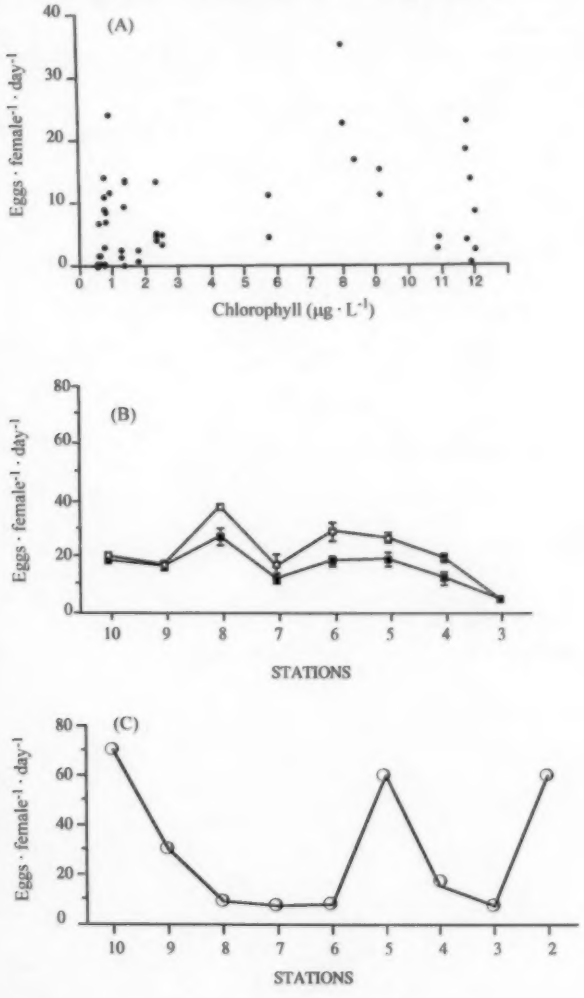
Fig. 7. (A) Relationship between egg production rate and chlorophyll concentration in the FSCREEN treatments in the type 2 experiments for all stations. (B) Egg production rates (means ± SD) in the FSCREEN treatments in the type 2 experiments at stations along the transect between Labrador and Greenland. Solid squares are the daily rates calculated over all 3 days of incubation and open squares are the rates for the first day. (C) In situ egg production rates estimated using the egg ratio method along the transect between Labrador and Greenland (see text for explanation).



Thus, in terms of the number of eggs produced, the rates that we observed over 3 days (range 5–38 eggs·female^{-1}·day^{-1}, average 16.5) were close to those observed for other populations of *C. finmarchicus* at similar or higher temperatures.

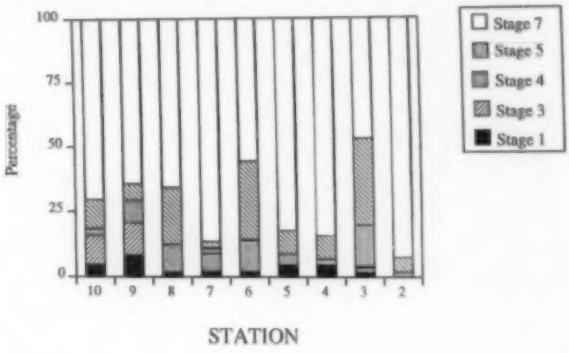
Comparison of experimental and estimated in situ rates of egg production

In situ egg production rates, calculated using the egg ratio method, showed a spatial pattern that was different from the one derived from experimental measurements (Fig. 7). According to the egg ratio method, the highest production rates were near the Greenland and Labrador coasts and at one station in the middle of the transect. The results obtained using the egg ratio method are influenced by hydrographic processes and predatory pressure and correspond to the combined effects over several days whereas experimental egg production rates correspond to daily rates in the absence of external factors. In the water column at stations 4 and 8, *C. finmarchicus* eggs seemed to be concentrated in the upper layers (30–40 m), although the highest densities were somewhat deeper than those of the females from which they were presumably derived (Fig. 5). The vertical distributions result from the interaction of a number of factors: egg production rates, sinking rates, hatching rates, and rates of consumption (cannibalistic or due to other predators). These in turn are affected by hydrographic factors (water temperature, density, turbulence) and biological ones (concentrations of food and predators).

Table 6. Results of stepwise multiple regression of egg production rates (FOOD treatment) versus feeding attributes.

Dependent	Variable entered	Coefficient	r^2	F	p
Egg production rate					
	Chlorophyll	2.17	0.394	8.84	<0.05
	Ingestion rate	−0.75	0.590	12.60	<0.001

Fig. 8. Percentage of female *C. finmarchicus* in the different gonad maturation stages along the transect between Labrador and Greenland.



Relationship between reproductive activity and in situ conditions

The hydrographic features along our transect in May–June 1994 were similar to those reported by Lazier and Wright (1993). Density gradients were steeper at stations near the coast of Labrador compared with those at stations on the rest of the transect, and there was a hydrographic front associated with the shelf break. The vertical stratification in the area near Labrador had apparently led to increased algal production and a large phytoplankton biomass, which was dominated by diatoms (J. Cabal, personal observation).

The abundances of both total copepods and *C. finmarchicus* were not obviously related to the hydrography and were lowest near Labrador and highest in the middle of the transect. The stage distribution within the population, however, did appear to be related to the hydrography. In the area close to pack-ice

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off Labrador the population was dominated by females along with stages CV and CIV whereas at stations on the other side of the front, stages CI, CII, and CIII were more abundant (Fig. 4B). If we assume a generation time of 109 days at T = 5°C between stages NII and CIII (Diel and Klein Breteler 1986), then in the central Labrador Sea and near Greenland, reproduction had started 2–3 months before our cruise. In these areas, it appears that *C. finmarchicus* had reproduced somewhat in advance of the spring bloom, as occurs among the sympatric species *C. hyperboreus* and *C. glacialis* (Conover 1965; Conover and Siferd 1993) which are also found in this region. Lipid reserves may sometimes be sufficient to sustain egg production without an external food supply, in the closely related species *Calanus heligolandicus* (Gatten et al. 1979, 1980). On both sides of the front, we found mature females in areas where early or prebloom hydrographic conditions (low chlorophyll concentrations, high nitrate concentrations) prevailed locally, suggesting that *C. finmarchicus* throughout the study area had matured to spawning stage in late winter, probably by using stored lipids. The apparent difference in the timing of the start of spawning between *C. finmarchicus* on either side of the front suggests that the overwintering sources of the two populations might have been different. Incidental observations suggested that female *C. finmarchicus* from waters to the west of the front, closer to Labrador, were more densely pigmented than were those from the other side of the front, but prosome lengths (3.03 ± 0.04 mm) and carbon and nitrogen contents of females were similar at all stations.

The values of *P*/*B* reported here are similar to those obtained by Hirche (1990) and Runge (1985*a*). The 3.08% body C·female^{-1}·day^{-1} put into eggs would require an ingestion rate of about 11% body C·female^{-1}·day^{-1} which represents 16.4 µg C·female^{-1}·day^{-1} or 328 ng Chl·female^{-1}·day^{-1}, for a carbon to chlorophyll ratio in the phytoplankton was 50. If we assume a concentration of 1 µg Chl·L^{-1}, then the copepods would have needed to filter 14 mL·female^{-1}·h^{-1}, if they were feeding continuously. Filtration rates in our incubations were close to 1 mL·female^{-1}·h^{-1}, but these may have been artificially low. For example, in the FSCREEN treatments, phytoplankton could sometimes be seen to be sinking through the screen, which would have led us to underestimate filtration rates (but not in vitro ingestion rates) because the vessels were mixed before sampling at the end of the incubation. In fact, on the same cruise, a series of experiments was conducted in which mixed copepod populations (containing about 50% *C. finmarchicus* females, numerically) were fed with natural seawater in large incubation vessels (8-L poylethylene carboys). Filtration rates were close to 1 mL·animal^{-1}·h^{-1} at station 2, where prebloom conditions applied and chlorophyll concentations were low, but higher (3–4 mL·animal^{-1}·h^{-1}) at stations 1 and 9, where chlorophyll concentrations were high (Head and Harris 1996). Thus, overall, it seems likely that ingestion of phytoplankton at stations where chlorophyll concentrations were high would have been sufficient to sustain the observed egg production rates. At stations where phytoplankton concentrations were low, if the higher filtration rates reported applied, then the observed egg production rates could have been sustained by ingestion of phytoplankton, but if the low filtration rates that we observed at station 2 applied, then ingestion of phytoplankton would have been inadequate. It is possible that an alternative food source was being used. For example, we cannot rule out microzooplankton as an alternative food resource because we did not assess its importance. Ohman and Runge (1994) have shown that ingestion of heterotrophic dinoflagellate and ciliates may be sufficient to fuel reproduction in the Gulf of St. Lawrence. Their study was conducted in the summer, however, well after the spring bloom, when microzooplankton levels would have been relatively high whereas our study was during the pre- and early bloom phases, when microzooplankton populations may well have been relatively much lower. Thus, on balance, it seems likely that at some stations, prestored lipid reserves were being used to fuel, or supplement, egg production in the central Labrador Sea.

In summary, when estimating instantaneous egg production rates by copepods, we suggest that it is probably more important to prevent cannibalism of the eggs by the females than to supply the latter with food, provided that incubations are of relatively short duration (i.e., 1 day). In addition, in situ egg abundances are not necessarily closely related to their production rate, presumably because of predation and hydrographic processes. Finally, in the Labrador Sea, egg production rates of *C. finmarchicus* were apparently not closely linked to in situ food concentrations, and it seems likely that stored energy reserves are important for reproduction of *C. finmarchicus* in this area.

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Discrimination of field-collected juveniles of two introduced dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) using mitochondrial DNA and shell morphology

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Abstract: We developed molecular markers to distinguish two species of exotic bivalves, the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis* sensu lato). Restriction analysis of a 710 base pair fragment of the COI mitochondrial gene showed a single restriction pattern for zebra mussels and a single restriction pattern for quagga mussels for each of the enzymes *Scr*FI, *Csp*6I, and *Sau*96I. This molecular analysis also confirmed that there were no sex-specific restriction patterns for either species. We then used our molecular markers to confirm the species identity of postmetamorphic and early juvenile stages (≥300 μm shell length) of zebra and quagga mussels from Lake Erie and the Rideau River (Ottawa, Ont.). Useful shell characteristics to discriminate between postmetamorphic and early juvenile stages (≥300 μm shell length) of zebra and quagga mussel included (*i*) overlap of valves at the posterior region, (*ii*) position of the dorsal point of curvature, (*iii*) angle of shell at the dorso-anterior region (hinge), and (*iv*) level of flatness of the ventral region (>2 mm shell length). Juveniles of approximately 300–700 μm shell length can be identified using the valve overlap criterion alone.

Résumé : Nous avons dévelopé des marqueurs moléculaires permettant de distinguer deux espèces de bivalves exotiques, la moule zébrée (*Dreissena polymorpha*) et la moule quagga (*Dreissena bugensis* sensu lato). L'analyse électrophorétique d'un fragment composé de 710 paires de bases provenant du gène mitochondrial COI a révélé un seul patron de restriction chez les moules zébrées de même qu'un seul patron de restriction chez les moules quaggas, et ce pour chacune des enzymes testées: *Scr*FI, *Csp*6I et *Sau*96I. Cette analyse moléculaire a aussi permis de confirmer qu'il n'y a pas de différence au niveau de patron de restriction entre mâles et femelles chez les deux espèces. Nous avons par la suite utilisé nos marqueurs moléculaires pour confirmer l'identification des stades post-métamorphiques et juvéniles (longueur de la coquille ≥ 300 μm) chez les moules zébrées et quaggas provenant du lac Erié et de la rivière Rideau (Ottawa, Ont.). Les critères morphologiques de la coquille permettent la discrimination entre les stades post-métamorphiques et juvéniles (longueur de la coquille ≥ 300 μm) de ces deux bivalves incluent *i*) le chevauchement des valves au niveau de la région postérieure, *ii*) la position relative du point de courbure dorsale, *iii*) l'angle de la région dorso-antérieure de la coquille (au niveau de la charnière) et *iv*) la morphologie de la région ventrale (longueur de la coquille > 2 mm). Les juvéniles d'environ 300–700 μm de longueur peuvent être indentifiés surtout pa la degré de chevauchement des valves.
[Traduit par la Rédaction]

Introduction

In the past decade, two bivalves, originating from Europe and belonging to the genus *Dreissena* (Dreissenidae), have been accidentally introduced to North America's Laurentian Great Lakes. The first record of the zebra mussel (*Dreissena polymorpha* (Pallas 1771)) was in Lake St.Clair in 1988 (Hebert et al. 1989). It quickly spread to all of the Great Lakes and the St. Lawrence River (Griffiths et al. 1991). In recent years, mussel colonization has expanded rapidly into connecting rivers and canals across eastern North America (Martel et al. 1995). May and Marsden (1992) reported a second species of dreissenid from Lake Ontario, the "quagga" mussel, which was identified as *Dreissena bugensis* (Andrusov 1897) by Rosenberg and Ludyanskiy (1994). The current North American distribution of the quagga mussel includes Lake Erie, Lake Ontario, and the St. Lawrence River (Mills et al. 1993) and thus extensively overlaps with that of the zebra mussel. Both mussels are native to rivers in the Black Sea region (Rosenberg and Ludyanskiy 1994) and are thought to have been introduced to North America by the discharge of ballast water from transoceanic vessels (Hebert et al. 1989; May and Marsden 1992). The quagga mussel resembles the zebra mussel in its morphology and life history, including the occurrence of a free-living planktonic larval stage (May and Marsden 1992), but differs with respect to habitat preference and physiology (Dermott and Munawar 1993; Domm et al. 1993; Mills et al. 1993; W.T. Claxton, unpublished data).

Dermott and Munawar (1993) reported a third dreissenid

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Table 1. Juvenile zebra (Z), quagga (Q), and "profunda" (P) mussel sample locations and numbers for both morphological and genetic studies.

Sample location	Depth (m)	Substrate type	No. of Z used for morphology	No. of Q used for morphology	No. of P used for morphology	No. of Z used for genetics	No. of Q used for genetics	No. of P used for genetics
Rideau River	4	Rock	20	—	—	13	—	—
Lake Erie (eastern basin)	1	Buoy	104	42	—	18	—	—
	1	Rock	—	77	—	5	18	—
	8	Rock/silt	—	—	—	—	6	—
	36	Silt	—	—	41	—	—	6
Lake Erie (western basin)	1	Buoy	52	—	—	—	6	—
Total			176	119	41	36	30	6

mussel phenotype taxon, tentatively named "profunda", in the deep waters of Lakes Erie and Ontario (>36 m); adults of this taxon lack a flaring posterior, are predominantly white, and occur in deeper water (Dermott and Munawar 1993). Spidle et al. (1994) examined allele frequencies at 11 polymorphic allozyme loci and found a considerable amount of genetic variation within the species *Dreissena bugensis* sensu stricto; they concluded that *D. bugensis* "profunda" was a phenotype of *D. bugensis* s.s. because their allele frequencies were almost identical. In contrast, Baldwin et al. (1996) reported that there were sequence differences (4 base pairs (bp)/619 bp) in the COI gene fragment between *D. bugensis* s.s. and *D. bugensis* "profunda". Unfortunately, they only sequenced a "few" individuals. Therefore, it is currently unclear whether these two mussels are sibling species or whether the variation in DNA sequence is within-species variation.

For the purposes of this study, "quagga" refers to shallow-collected *D. bugensis* and *D. bugensis* "profunda" refers to the deepwater "profunda" mussel reported by Dermott and Munawar (1993). Within the scope of this paper, *D. bugensis* s.s. and *D. bugensis* "profunda" were treated as a single species unless specifically stated.

Although the morphology of both adult and larval stages of zebra and quagga mussels has been described, there is no published material available on shell characters that can be used to reliably distinguish between their early postmetamorphic and early juvenile stages. The early juvenile is the first benthic stage and is often numerically dominant on natural and man-made substrates, especially following episodes of larval settlement. The ability to confidently identify early postmetamorphic or juvenile stages, to the species level, is important to biologists interested in larval settlement and benthic studies. Moreover, species discrimination may be important to engineers because control methods may differ according to species.

Our objective was to find morphological characters that could be used to differentiate early juvenile stages of the zebra and quagga mussels. Our strategy was to differentiate individual mussels by restriction fragment length polymorphism (RFLP), a powerful tool to differente species without obvious morphological differences (Avise 1994). We used specimens collected from the field that were tentatively identified on the basis of presence or absence of valve overlap and the degree of ventral flatness. Our identifications were verified using restriction enzyme analysis of the mitochondrial gene cytochrome *c* oxidase subunit I (COI) in juvenile zebra and quagga mussels. The species-specific restriction pattern was first obtained from positively identified mature adult specimens using shell morphology.

In addition to using restriction enzyme analysis for species identification, inheritance of mtDNA was also examined. Historically, mitochondrial inheritance has been thought to be almost exclusively maternal. However, a number of researchers have found that the mitochondrial genome of males of several species of *Mytilus* also exhibits paternal inheritance, with respect to mtDNA haplotype (Fisher and Skibinski 1990; Hoeh et al. 1991; Zouros et al. 1992). As a result, the typical pattern of maternal inheritance of mtDNA has recently been called into question, especially in bivalves. In light of this recent evidence for atypical mtDNA inheritance in *Mytilus*, restriction analysis was used to determine if restriction site differences existed between the sexes of zebra and quagga mussels. This was done to establish whether paternal mitochondrial inheritance occurs in zebra or quagga mussels.

Materials and methods

Field sampling of mussels

Juvenile mussels (*Dreissena* spp.) were collected from two regions in Ontario, Canada: Lake Erie (eastern and western basins) and the northern Rideau River, near Ottawa (Table 1). Mussels collected from the benthos of the eastern basin of Lake Erie (Long Point Bay, offshore of Port Dover) were sampled on September 24 and October 24, 1994, using a Ponar grab (0.055 m2), at water depths of 1 m (rocky), 8 m (silty substrate), and 36 m (silty substrate). Mussel samples from 36 m morphologically resembled *D. bugensis* "profunda", as described by Dermott and Munawar (1993). Mussels were also collected from navigation buoys in the eastern basin of Lake Erie, offshore of Nanticoke and Port Colborne (Table 1). In the western basin, juvenile zebra and quagga mussels were collected from two navigation buoys in the Pelee Passage, southwest of Point Pelee National Park, between November 1992 and December 1993 (Table 1). Zebra mussels collected from the Rideau River were sampled at Hartwells Lock Station, near Ottawa, on October 16, 1994.

After collection, individual mussels from all locations were transported live to the mollusc laboratory of the Canadian Museum of Nature. They were sorted and tentatively identified to species, using the characters of shell overlap and degree of ventral flatness only. Individuals undergoing shell morphometric analysis only were preserved in 70% ethanol (Table 1). Individuals >7 mm undergoing RFLP analysis had the tissue removed from the shell and then frozen at –70°C. Individuals <7 mm were frozen whole at –70°C. All frozen specimens were shipped to the University of Guelph on dry ice for DNA analysis.

RFLP analysis was carried out on juvenile zebra (N = 36; 2.2–3.2 mm shell length) and quagga mussels (N = 36; 0.8–3.0 mm shell length) (Table 1). A total of 18 juvenile zebra and 18 juvenile

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quagga mussels were analyzed with respect to both shell morphometrics and RFLP.

The adult mussels used in this study were collected in Long Point Bay, in the eastern basin of Lake Erie. Twenty-five adult zebra mussels (13 female, 12 male) and 30 adult quagga mussels (15 female, 12 male) were collected from rock substrate, at a depth of 1 m, and brought to the University of Guelph. The sex of each adult mussel was determined using light microscopy (40×). A small piece of gonad was examined for the presence of maturing eggs or sperm. Adults were frozen whole at −70°C after sex determination. Restriction analysis of the COI mitochondrial gene fragment was then carried out on the male and female adult mussels. This analysis established the species-specific restriction pattern for both zebra and quagga mussels, for each restriction enzyme. In addition, it was possible to determine if sexual dimorphism in restriction pattern existed in either species.

Isolation of dreissenid mtDNA

Isolations of mtDNA were carried out using 2.0 mg (wet mass) of adult visceral tissue, or the intact juvenile (shell and soft tissue). Isolation methods were the same for both adult and early juvenile dreissenids, using a protocol developed by Maureen Krause (Natural Science Department, Southampton College, Southampton, N.Y., personal communication). The dissected visceral tissue (or the intact juvenile) was placed in 400 µL of a homogenization buffer solution containing 1× SSC (0.15 M NaCl, 0.015 M citric acid (trisodium dihydrate)), 1.1% sodium dodecyl sulfate (SDS), and 0.5 mg proteinase K/mL. Tissue was incubated at 55°C for 12 h. The homogenate was then mixed with 130 µL of 5 M NaCl and 44 µL of 24:1 methylene chloride – isoamyl alcohol (MCIA) and centrifuged at 2000*g* for 5 min and then at 6000*g* for 10 min. The supernatant was removed and 400 µL of MCIA added. The mixture was then centrifuged at 6000*g* for 5 min. An ethanol precipitation was carried out on the resulting supernatant. The dried pellet was dissolved in 30 µL of sterile distilled water.

Polymerase chain reaction (PCR) of dreissenid mtDNA

A set of two PCR primers for the COI mitochondrial gene were used to amplify the mtDNA fragment for both mussels (Folmer et al. 1994). These primers produced a 710-bp fragment of mtDNA. The PCR was performed as described by Innis et al. (1988). One microlitre of the isolated DNA was used for the template for the PCR. The concentration of MgCl2 during PCR was 1.5 mM. PCR was carried out for 35 cycles at an annealing temperature of 46°C and an extension temperature of 72°C for 45 s.

Restriction analysis

Restriction analysis of the COI gene was carried out using three restriction enzymes: *Scr*fI, *Csp*6I, and *Sau*96I. Restriction enzyme digests consisted of 4.0 µL of PCR product, 4.5 µL of sterile distilled water, 1.0 µL of 10× buffer, and 0.5 µL of the appropriate enzyme. Digests were incubated at 37.0°C for 18 h, mixed with xylene cyanole at 14%, and then loaded onto 2% agarose gels containing 0.04 mg ethidium bromide/100 mL. Electrophoresis was carried out for 2 h at 60 mV in standard TBE buffer. Gels were visualized under UV light and photographed.

Morphological characters of the juvenile shell

The shells of zebra and quagga mussels (size range 300 µm – 12 mm) were assessed for six qualitative and quantitative characters. Linear combinations of the quantitative characters were used to discriminate the two species.

A morphometric analysis of juvenile zebra and quagga mussel whole shells was conducted using both dried and wet specimens. The following measurements were taken on each individual (Fig. 1). (1) L: shell length, the longest antero-posterior dimension of the shell. (2) H: shell height, the longest dorsal-ventral dimension of the shell. (3) PDC: point of dorsal curvature, the point at which the antero-dorsal margin (hinge area) began to rapidly curve downwards to create the dorsal/dorso-posterior shell margin. The PDC was expressed in millimetres as a point along the antero-dorsal shell axis. (4) ANGLE: angle of the anterior-dorsal section at the hinge level, the angle formed by a line connecting the top of the umbo and the PDC of the shell (Fig. 1). Measurements of (1)–(4) were taken using Genteel/SigmaScan software, with a digitizer, used in conjunction with an Olympus SZH-DA drawing attachment.

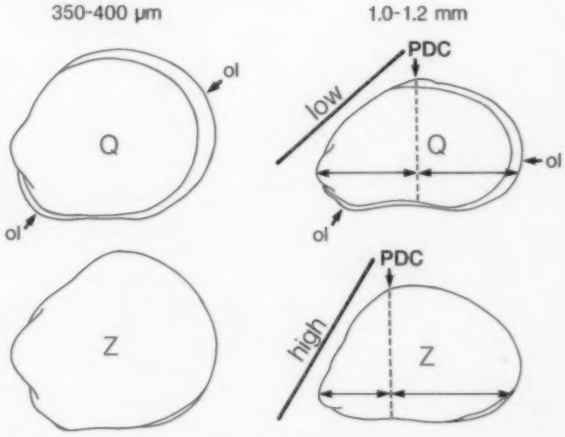

Fig. 1. Shell characters used to differentiate between early postmetamorphic or juvenile stages of quagga (Q) and zebra (Z) mussels on idealized specimens: valve overlap (ol), point of dorsal curvature (PDC), angle (low or high).

Qualitative morphological characters used to discriminate juvenile stages of zebra mussels from those of quagga mussels included (5) valve overlap, the difference in length, or the degree of overlap, between the right and left valve and (6) degree of flatness, whether or not the ventral margin of the shell is flat or curved (Fig. 1).

Statistics

The PDC and ANGLE of the dreissenid mussels were compared using analysis of covariance (ANCOVA) and analysis of variance (ANOVA), respectively. Discriminant analysis was done on the variables L, H, PDC, and ANGLE using the program SYSTAT (1992) to see how successfully a linear combination of these variables could separate early juveniles of zebra mussels from quagga mussels. This was done in two steps. First, a total of 336 juvenile specimens that had been tentatively identified using the characters of valve overlap and degree of flatness of the ventral region were used to construct the discriminant function. Then the validity of the function was tested using an additional 18 zebra and 18 quagga mussels, whose identity was later confirmed using restriction analysis.

Results

Restriction analysis of mtDNA

Restriction analysis of the COI mitochondrial gene of adult and juvenile zebra and quagga mussels showed one distinct restriction pattern per species for each enzyme tested. The restriction pattern corresponded perfectly to the tentative species separation made using morphology and morphometry.

A clear restriction site polymorphism between adults of the two species was shown when the COI fragment was digested with *Scr*fI (Fig. 2*a*). All 25 adult zebra mussels produced three mtDNA fragments of approximately 150, 200, and 450 bp

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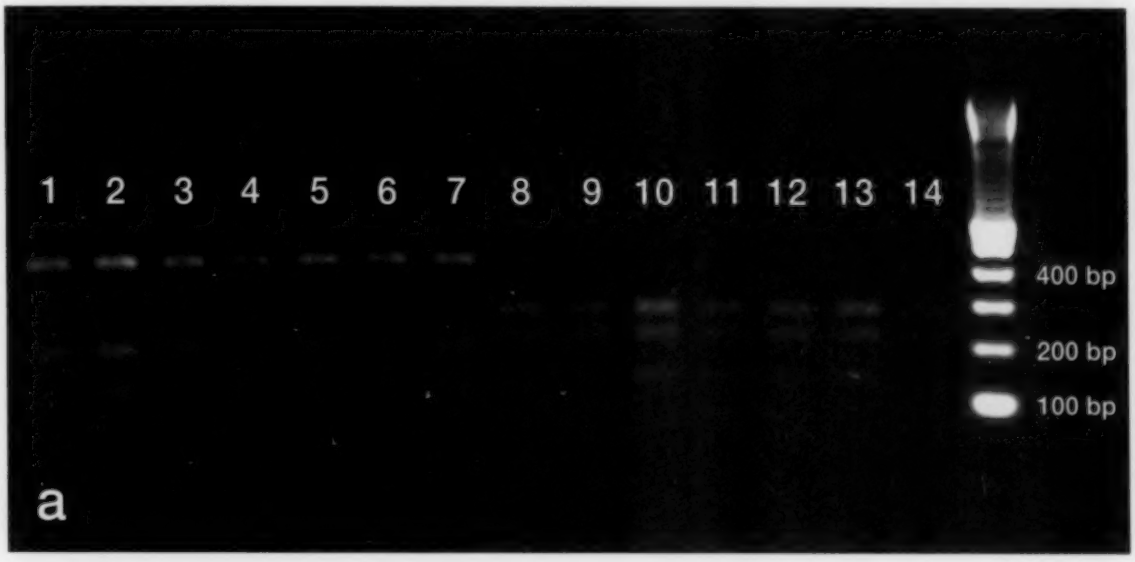
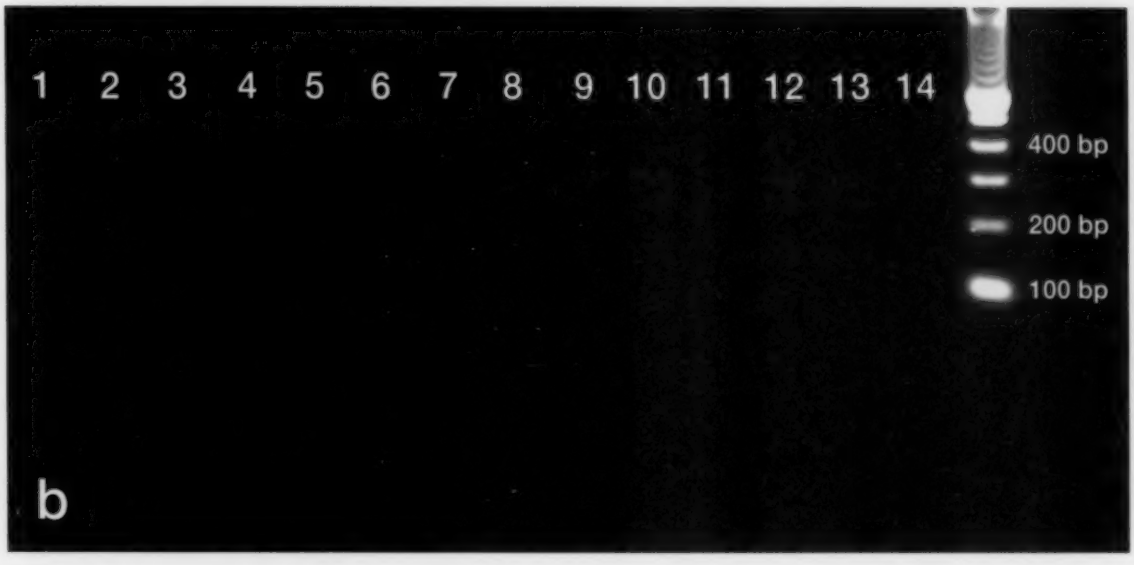
Fig. 2. Restriction digest of a fragment of the COI mitochondrial gene of zebra and quagga mussels with *Scr*fI, visualized with ethidium bromide staining. (*a*) Lanes 1–7, adult zebra mussel; lanes 8–14, adult quagga mussel. (*b*) Lanes 1–7, juvenile zebra mussel; lanes 8–14, juvenile quagga mussel.





(Fig. 2*a*, lanes 1–7). All 30 adult quagga mussels' mtDNA produced four mtDNA fragments of approximately 50, 150, 200, and 250 bp (Fig. 2*a*, lanes 8–14). Both species of juvenile mussels ($N = 36$ zebra; $N = 36$ quagga) showed the same polymorphism that was present in adult zebra and quagga mussels (Fig. 2*b*).

No variation in the restriction pattern was noted between the sexes of either mussel species using *Scr*fI or the other two restriction enzymes tested (*Csp*6I, *Sau*96I) (Fig. 3). All three restriction enzymes showed different patterns for the two species (Table 2).

Juvenile shell morphology

Morphological and morphometric differences between juvenile shells of zebra and quagga mussels were similar, distinct, and consistent among sampling locations (Fig. 4).

(i) Valve overlap

Shell valves of zebra mussel were flush and of equal length at the posterior shell margin. However, there was some valve overlap in the ventro-posterior corner of the shell. In intact quagga mussels the right shell valve overlapped the left, in the posterior region of the shell. Overlap occurred in specimens

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Fig. 3. Restriction digest of a fragment of the COI mitochondrial gene of adult male and female zebra and quagga mussels with *Scr*fI, visualized with ethidium bromide staining. Lanes 1–6, male quagga mussel; lanes 7–12, female quagga mussel; lanes 13–18, male zebra mussel; lanes 19–23, female zebra mussel.

Table 2. Approximate fragment sizes (bp) generated from the COI mitochondrial gene of zebra and quagga mussels by restriction enzymes.

Enzyme	Recognition site	Zebra mussels	Quagga mussels
*Scr*fI	CCNGG	100	50
		200	150
		450	200
			250
*Csp*6I	GTAC	250	150
		450	550
*Sau*96I	GGNCC	150	100
		200	200
		400	350

>350 μm (Figs. 1 and 4*a*). Valve overlap created a thin but distinct crescent of shell, extending beyond the end of the left valve, from the dorso-posterior to the ventro-posterior region. In many specimens, it also extended along the ventral region to the umbo, forming a narrow band of overlapping shell (Fig. 1). The overlapping crescent of the right valve often showed evidence of a broken margin. However, the overlap was usually still visible at higher magnification. In *D. bugensis* "profunda" the overlapping crescent of shell often appeared narrower and more fragile than in specimens collected from shallower depths. In most *D. bugensis* "profunda" juveniles, the shell overlap in the posterior region was damaged. This resulted in an irregular posterior shell margin. In well-preserved specimens, the valve overlap across the entire posterior shell margin was the most conspicuous diagnostic shell character for postmetamorphic quagga specimens of shell length <1.0 mm (Figs. 1, 4*a*, and 4*b*).

(ii) Point of dorsal curvature (PDC)

The PDC position differed significantly in zebra and quagga mussels (ANCOVA, $P < 0.001$). Juvenile quagga mussels from deep and shallow sites showed a mean PDC/L of 0.492 ($N = 142$, size range 0.48–10.6 mm, SD = 0.0480), while juvenile zebra mussel showed a mean PDC/L value of 0.339 ($N = 158$, size range 0.55–10.0 mm, SD = 0.0520). No significant difference in PDC was noted between juvenile quagga mussel and *D. bugensis* "profunda" (ANCOVA, $P = 0.112$). Some overlap in PDC/L values occurred between species. PDC could be used alone as a diagnostic character for juveniles >0.7 mm shell length (Figs. 4*a*, 4*b*, and 5).

(iii) Angle of dorsal margin (ANGLE)

The angle of the dorso-anterior margin (just above the umbo to the PDC) was significantly greater in zebra mussel shells than in quagga mussel shells (ANOVA, $P < 0.001$) (Figs. 4*b–4i*, 6). The mean angle of the dorsal margin was 60.0° for juvenile zebra mussels ($N = 158$, size range 0.55–10.00 mm, SD = 4.46) and 45.5° for juvenile quagga mussels ($N = 142$, size range 0.48–10.6 mm, SD = 4.00). This angle was only useful for differentiation in mussels ≥0.50 mm (Figs. 1 and 4*a*). No significant difference was noted in the angle of the dorso-anterior margin between juvenile quagga mussel and juvenile *D. bugensis* "profunda" (ANOVA, $P = 0.329$).

(iv) Flatness of ventral region

This character is useful for individuals >2 mm in shell length, since juvenile mussels of both species showed a rounded ventral shell in individuals below that size (Figs. 4*a–4d*). For shell lengths >2 mm, the ventral surface of juvenile zebra mussel was distinctly flattened in the dorsal ventral plane, characteristic of the adult mussel (Figs. 4*e–4i*). Both quagga mussels and *D. bugensis* "profunda" continued to show a rounded ventral surface as shell length increased.

Statistics

There were significant correlations (Table 3) between PDC and shell length (Fig. 5) and between PDC and shell height. However, ANGLE was not significantly correlated with H or L and was only weakly correlated with PDC (Table 3).

The discriminant analysis resulted in a canonical correlation of 0.896. The canonical loading was greatest for ANGLE

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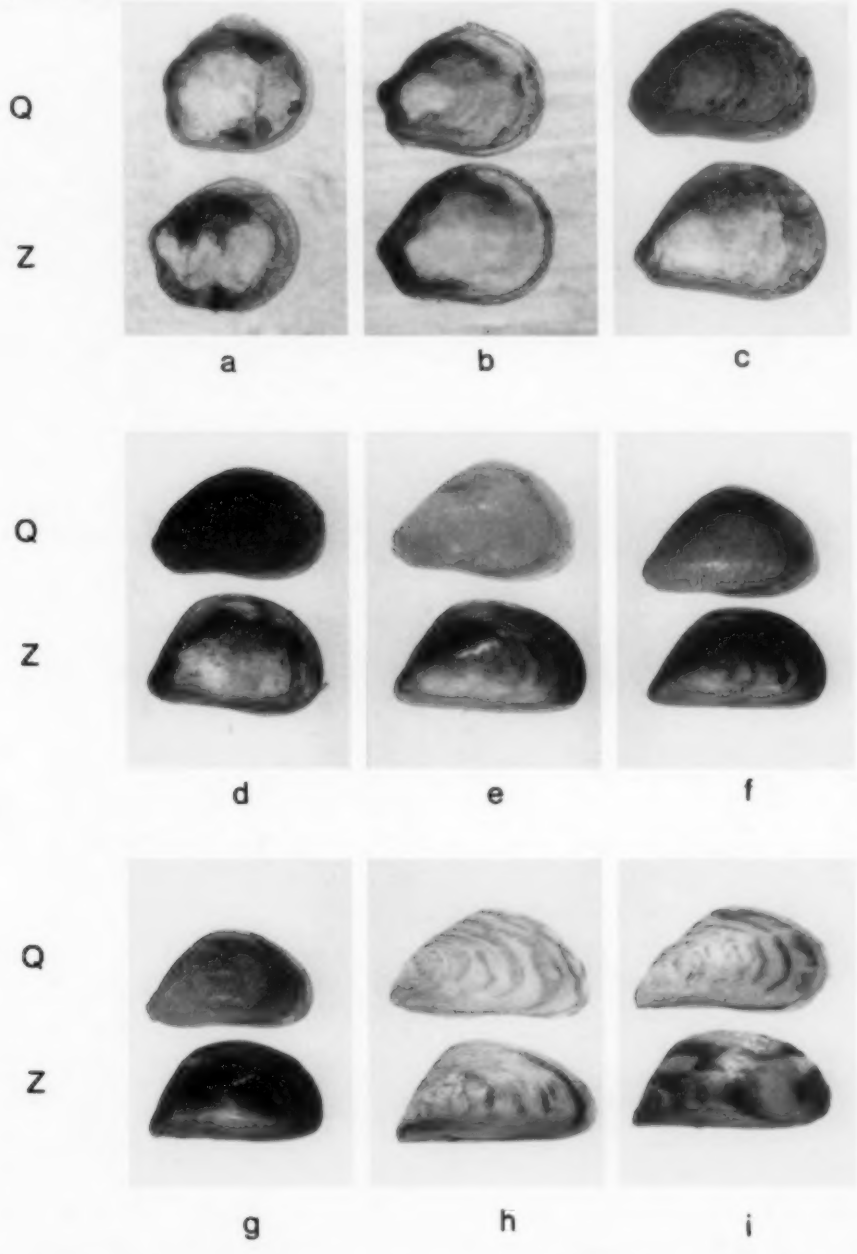
Fig. 4. Microphotographs of paired similar-sized juveniles of quagga (Q) and zebra (Z) mussels demonstrating diagnostic shell characters through ontogeny. Shell length (mm) as measured with a stereomicroscope–digitizer measurement system: (*a*) Q = 0.34, Z = 0.35; (*b*) Q = 0.57, Z = 0.61; (*c*) Q = 0.98, Z = 1.02; (*d*) Q = 1.33, Z = 1.36; (*e*) Q = 2.16, Z = 2.26; (*f*) Q = 3.10, Z = 3.14; (*g*) Q = 4.74, Z = 4.93; (*h*) Q = 7.44, Z = 7.53; (*i*) Q = 9.67, Z = 9.58. The narrow crescent of shell overlap in the posterior region of the quagga dissoconch is clearly visible in most photographs, especially in Fig. 4*b*.



(0.785), moderate for PDC (–0.109), and smallest for H (–0.006) and L (0.014). The discriminant function (Table 4) correctly classified 96.5% of zebra mussels and 98.1% of quagga mussels that had been used to construct it. These individuals had previously been assigned to a species, based on the presence or absence of valve overlap and degree of flatness.

The validity of the discriminant function was tested using 18 juvenile zebra and 18 juvenile quagga mussels, which were all later identified using restriction analysis. The function correctly classified 88.9% of the 18 zebra mussels and 100% of the 18 quagga mussels (Table 5). The misclassified zebra mussels had an angle of dorsal margin measurement that was too

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Fig. 5. Relationship between the PDC and shell length for zebra (triangles) ($N = 158$) and quagga mussels (circles) ($N = 142$).

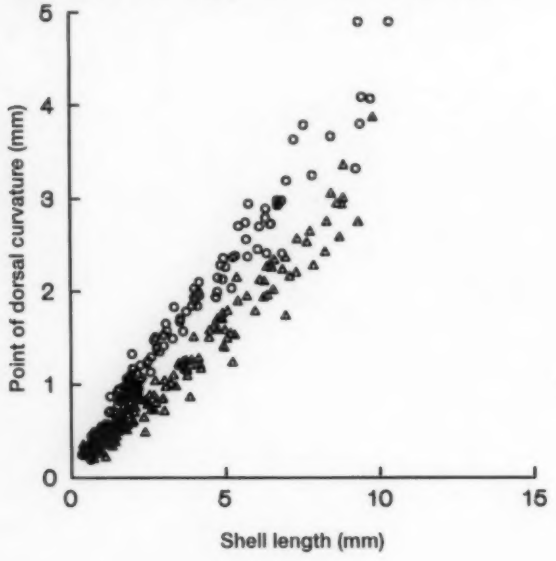
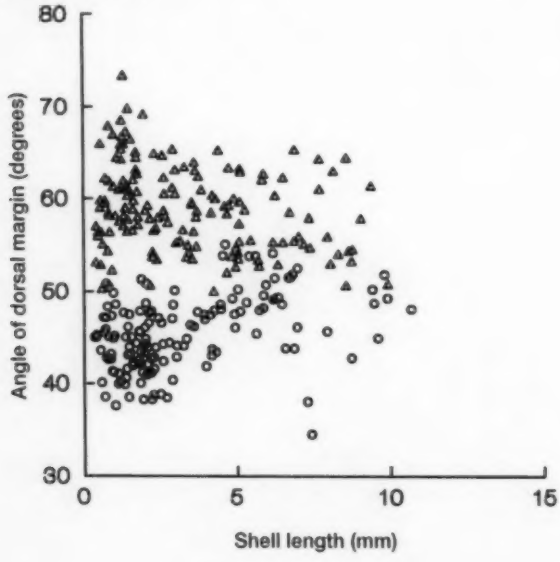


Fig. 6. Relationship between angle of the antero-dorsal shell margin and shell length in zebra (triangles) ($N = 158$) and quagga mussels (circles) ($N = 142$).



low. Accurate measurement of this character requires great care.

Discussion

Restriction analysis of mtDNA

Our analysis of a fragment of the COI mitochondrial gene clearly showed restriction site differences between the zebra and quagga mussels, distinguishing the species at both the adult and postlarval stages. Restriction site differences remained consistent, regardless of the sample location of the test mussels. Therefore, it was possible to accurately identify the species composition of mussel populations mixed with respect to origin and stage of development. Restriction analysis also showed that the discriminant classification function, using four morphological shell characters, was able to differentiate juvenile zebra and quagga mussels.

Historically, maternal mitochondrial inheritance has been found to be the most common. However, paternal inheritance occurs in males in several species of *Mytilus* (Fisher and Skibinski 1990; Hoeh et al. 1991; Zouros et al. 1992). Zouros et al. (1994) explained sex-specific restriction patterns in *Mytilus* by showing that mitochondrial inheritance in *Mytilus edulis* can be both maternal and paternal in the male and exclusively maternal in the female. As a result, the female is homoplasmic with respect to mtDNA type, while the male is usually heteroplasmic.

Table 3. Correlation between shell morphometric characters for all specimens combined.

	L	H	PDC	ANGLE
L	1.000			
H	0.993[a]	1.000		
PDC	0.949[a]	0.958[a]		
ANGLE	0.036	0.027	–0.182[b]	1.000

[a]Significant, $P < 0.001$, $N = 300$.
[b]Significant, $P < 0.005$, $N = 300$.

Table 4. Group classification function coefficients.

Variable	Zebra mussels	Quagga mussels
L	18.9	9.918
H	–45.79	–34.18
PDC	16.2	23.77
ANGLE	3.96	3.10
Constant	–114.9	–72.0

Note: The values for each measurement of an individual specimen are multiplied by the appropriate coefficient and summed together and then added to the constant. The calculation is done separately for each species using the appropriate coefficients. The specimen is then assigned to the species that gives the largest value for the group classification function.

Table 5. Results from using the group classification function from the discriminant analysis on the 36 specimens that had *not* been used to estimate it.

	Molecular data			
	Zebra mussel pattern		Quagga mussel pattern	
Function	Overlap	Flush	Overlap	Flush
Zebra mussels	0	16	0	0
Quagga mussel	0	2	18	0
% correct	—	88.9	100	—

Note: Morphometric variables used in the discriminant function were measured from photographs. These test specimens also had their valve overlap evaluated and their restriction pattern scored when the COI fragment was digested with the enzyme *Scr*fI. As described in the text the undamaged shells of zebra mussels have flush valves and the undamaged shells of quagga mussels have the right valve overlapping the left.

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The most interesting finding was that the female haplotype from *Mytilus trossulus* was more similar to the female haplotype from *M. edulis* than to the male haplotype from *M. trossulus* (Wenne and Skibinski 1995). In our study, the lack of restriction site differences noted between the sexes of either species suggests that mitochondrial inheritance is exclusively maternal in both dreissenid mussels.

Juvenile shell morphology

Our study indicates that it is possible to discriminate between field-collected, early postmetamorphic, and juvenile stages (≥300 μm) of zebra and quagga mussels using four morphological shell characters that are visible using a stereomicroscope (Fig. 1). In well-preserved specimens, valve overlap is the most reliable criterion for distinguishing quagga mussels and *D. bugensis* "profunda" (recently metamorphosed (≥300 μm) to late juveniles (10 mm)) (Nichols and Black 1994) from zebra mussels. Posterior valve overlap can even be observed in undamaged adult *D. bugensis* "profunda" (Dermott and Munawar 1993).

Flatness of the ventral region of the juvenile shell is the most reliable criterion for distinguishing quagga mussels and *D. bugensis* "profunda" (>2 mm) from zebra mussels. Degree of flatness and carina development become more pronounced with ontogeny in the zebra mussel but not in the quagga mussel or *D. bugensis* "profunda". These two characteristics have been used extensively to differentiate adult zebra and quagga mussels by many authors (May and Marsden 1992; Dermott and Munawar 1993; Pathy and Mackie 1993; Rosenberg and Ludyanskiy 1994).

Although the four morphological shell characters shown in this study are diagnostic for the two species, considerable phenotypic plasticity in all the characters, except valve overlap, exists even within single populations. This phenotypic plasticity in shell morphology has previously been noted for dreissenid bivalves (Pathy and Mackie 1993; Rosenberg and Ludyanskiy 1994). Phenotypic plasticity in the shell shape of a marine bivalve, *Mya arenaria*, changes with growth rate and sediment type (Newell and Hidu 1982). Similar plasticity is also likely in other bivalves.

Our discriminant analysis showed that a classification function incorporating length, height, PDC, and angle classified specimens almost identically as had been done using valve overlap alone. The overlapping crescent of the right valve can be broken off in adult quagga mussels, so it is important not to rely on it exclusively. Our classification functions are a good check that a specimen has been identified correctly.

Our primary purpose was to use restriction enzyme analysis to find reliable diagnostic shell characters to differentiate juvenile zebra and quagga mussels. This was accomplished, but differentiation between quagga mussels and *D. bugensis* "profunda" was not possible with the shell characters we used. Restriction analysis of COI was also unsuccessful in differentiating between these mussels. However, COI is the most conservative protein-coding gene in the mitochondria, and RFLP analysis of this gene is unlikely to be useful for differentiating species that have been separated for more than 1 million years (Avise 1994). Based on results from protein electrophoresis (Spidle et al. 1994), quagga mussels and *D. bugensis* "profunda" are certainly very closely related taxa. Therefore, further study, using a faster-evolving gene, may reveal whether they are sibling species or whether they represent a highly variable population.

The ability to cosnfidently identify and differentiate early postmetamorphic and juvenile mussels may be useful in future studies on larval settlement in Great Lakes dreissenids. Early postmetamorphic stages are often numerically dominant in benthic samples, especially after episodes of larval settlement. Discrimination between early postmetamorphic stages of zebra and quagga mussels is important in the investigation of species-specific patterns of larval settlement. Discrimination of early settlers is particularly critical for settlement and recruitment studies that take place in locations that have colonies of both dreissenids.

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Bioenergetics of life history strategies and the comparative allometry of reproduction

Kevin McCann and Brian Shuter

Abstract: Winemiller and Rose (1992, Can. J. Fish. Aquat. Sci. 49: 2196–2218) showed that fish life history data lie on a two-dimensional triangular surface, embedded in the three-dimensional space established by the following biological attributes: (*i*) age at maturity, (*ii*) fecundity, and (*iii*) juvenile survivorship (as measured by the presence/absence of parental care). The vertices of this triangular surface define three endpoint strategies (equilibrium, opportunistic, and periodic) that Winemiller and Rose viewed as boundary strategies for all fish life histories. This paper extends these ideas by showing empirically that (*i*) the allometric relationship linking peak ovary weight to adult body weight differs across endpoint strategies, (*ii*) the allometric relationship linking age at 50% maturity to adult body weight is the same across endpoint strategies with the exception of the opportunistic strategy, and (*iii*) the allometric relationships characteristic of Winemiller–Rose endpoint strategies, plus that of a fourth strategy (composed of the genera *Salmo* and *Onchorynchus*), combine to form constraints that bound data on reproductive effort from a sample of species that represent a broad range of fish life history strategies. We offer some hypotheses as to why such constraints might exist.

Résumé : Winemiller et Rose (1992, J. can. sci. halieut. aquat. 49 : 2196–2218) ont montré que les données sur le cycle vital des poissons se situent sur une surface triangulaire bidimensionnelle incluse dans un espace tridimensionnel établi par les caractéristiques biologiques suivantes : *i*) l'âge à maturité, *ii*) la fertilité et *iii*) la survie des juvéniles (telle que mesurée par la présence ou l'absence de soins parentaux). Les sommets de cette surface triangulaire définissent trois stratégies finales (équilibre, opportuniste et périodique) que Winemiller et Rose voient comme des stratégies ultimes pour tous les cycles vitaux de poisson. Le présent article constitue un prolongement de ces idées en montrant empiriquement que *i*) la relation allométrique liant le poids ovarien maximal au poids corporel de l'adulte diffère selon les stratégies ultimes, *ii*) la relation allométrique liant l'âge à 50% de maturité au poids corporel de l'adulte est le même dans toutes les stratégies ultimes sauf la stratégie opportuniste et *iii*) les relations allométriques caractéristiques des stratégies ultimes de Winemiller et Rose, plus celle d'une quatrième stratégie (composée des genres *Salmo* et *Oncorhynchus*), se combinent pour former des contraintes qui lient les données à l'effort de reproduction à partir d'un échantillon d'espèces qui représentent une vaste gamme de stratégies de cycles vitaux de poisson. Nous formulons certaines hypothèses pour tenter d'expliquer pourquoi de telles contraintes pourraient exister.
[Traduit par la Rédaction]

Introduction

MacArthur and Wilson (1967) introduced *r–K* theory to account for both the wide range of life history strategies observed among animals and the observed linkages between specific strategies and specific habitats. The *r–K* model suggests that observed life history strategies span a one-dimensional continuum. The continuum is bounded by two endpoint strategies: the *r*-strategy, characteristic of small, high-fecundity animals, and the *K*-strategy, characteristic of large, low-fecundity animals. Moving along this continuum, from *r*-strategists toward *K*-strategists, implies moving from small animals with high reproductive rates to large animals with low reproductive rates. It also implies moving from disturbed environments, where the high reproductive rates of *r*-strategists provide greater fitness, to constant or predictable environments, where the more competitive *K*-strategists have a greater fitness.

Although *r–K* theory has remained central to life history studies, it has been plagued by two major problems. First, it is difficult to forge a direct connection between *r–K* models and empirical studies because the two parameters (i.e., *r*, the intrinsic rate of population increase, and *K*, the population carrying capacity) that define such models are simplified composites that reflect the joint influences of many separate attributes of a population (i.e., age-specific maturity, fecundity and mortality schedules, and their dependence on various physiological and environmental factors). Second, observed variation in life history strategies is too complex to be explained by *r–K* theory alone (e.g., Stearns 1977).

Recently, Winemiller and Rose (1992) extended the *r–K* model to a two-dimensional continuum. Their extended model was based on the analysis of the variation in 16 life history traits exhibited by a large and representative sample of North American freshwater and marine fish species (216 species from 57 families). They found that most of the observed variation (91%) was captured in the variation of three particular life history traits: age at maturity, fecundity, and juvenile survivorship (as measured by the presence/absence of parental care). Within the three-dimensional life history space defined by these three attributes, the data from individual species were

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Table 1. Species involved in literature search by strategy.

Strategy	Species
Opportunistic	Anchovies, silversides, sardines, mosquitofish
Periodic	Walleye, yellow perch, striped bass, winter flounder, pike, large suckers, any extremely large fish with high fecundity
Equilibrium	Sunfish, bullheads, black bass, smallmouth bass, largemouth bass, ariid catfish, madtoms,[a] darters[a]

[a]Only those species with nest defense.

restricted to a two-dimensional triangular surface. The vertices of this triangular surface mark boundaries for the range of life history strategies exhibited by the species in their data set. Winemiller and Rose (1992) defined these three boundary points as *endpoint strategies* and provided the following definitions as summaries of the characteristic biological and habitat attributes for species associated with each strategy: (*i*) periodic strategist (e.g., striped bass (*Morone saxatilis*)): these are large-bodied fishes with late maturation, high fecundity per spawning event, and low juvenile survivorship (i.e., no parental care); they exhibit some attributes of the classical *r*-strategist (e.g., high fecundity) but differ in that they are large and long-lived; they inhabit predictable, seasonal environments; (*ii*) opportunistic strategist (e.g., bay anchovy (*Anchoa mitchilli*)): these are small-bodied fishes with early maturation, low fecundity per spawning event but several spawning events spread over a prolonged annual spawning season, and low juvenile survivorship (i.e., no parental care); they exhibit most of the attributes of the classical *r*-strategist (e.g., small body size, early maturation, short life span) but differ in that fecundity per spawning event is low; they inhabit highly disturbed and unpredictable environments; (*iii*) equilibrium strategist (e.g., bantam sunfish (*Lepomis symmetricus*)): these are small- to medium-bodied fishes with moderate maturation age, low fecundity per spawning event, and high juvenile survivorship (i.e., provides parental care); they inhabit constant environments.

Thus, the Winemiller–Rose model extends the *r*–*K* model by recognizing three endpoint strategies, rather than two: the single *r*-strategy is split and the distinctions that separate periodic and opportunistic strategies are recognized; the *K* strategy is redefined along narrower lines as the equilibrium strategy. Most importantly, the Winemiller–Rose model is defined in terms of three measurable demographic parameters (i.e., age at maturity, fecundity, and juvenile survivorship) and hence can be more easily linked to empirical observations.

The demographic parameters used by Winemiller and Rose (1992) are direct reflections of the ways in which fish allocate energy to reproduction: age at maturity reflects the delay in switching available energy from individual growth to reproductive activities, fecundity per spawning event reflects the direct allocation of energy by an adult to offspring, and the presence/absence of parental care reflects the indirect allocation of energy by an adult to offspring, in terms of activities designed to enhance offspring survival. Attributes associated with the bioenergetics of an animal typically exhibit allometric relationships with body size, and in fish, both age at maturity and fecundity exhibit such relationships (Weatherley and Gill 1987; Paloheimo and Dickie 1966*a*, 1966*b*). The following rationale shows that strategy-specific differences in these allometric relationships are to be expected: (*i*) Prothero (1986) pointed out that behind every scaling study lies the tacit assumption of structural and functional similarity; organisms that function differently will *often* exhibit different allometric relationships; (*ii*) the Winemiller–Rose model is founded on the recognition of significant differences among endpoint strategies in the allocation of energy to reproduction; (*iii*) hence, allometric relationships involving attributes associated with the allocation of energy to reproduction are likely to exhibit strategy-specific differences.

Table. 2. Criteria that data must meet by strategy.

	Strategy		
Condition	Periodic	Opportunistic	Equilibrium
Parental care (nest defense)	No	No	Yes
Spawning frequency	One	Multiple	One

In this paper, we develop empirical tests of the hypothesis that allometric relationships for fecundity and age at maturity differ across the endpoint strategies identified in the Winemiller–Rose model.

Methods

Data standards

Our objective was to compare allometric relationships for fecundity and age of maturity across the three endpoint strategies defined by Winemiller and Rose 1992). The raw material for such an empirical study consists of population-specific fecundity and age at maturity data, as reported in the primary scientific literature. To use these data in our comparisons, we needed to develop an algorithm that would reliably categorize population-specific data by endpoint strategy. This algorithm would allow for the fact that, among fish, life history parameters show considerable intraspecific variation and thus the best representatives of endpoint strategies would be seen at the population level. We used the following algorithm: (*i*) we established a list containing species whose "typical" life history characteristics closely matched one of the Winemiller–Rose endpoint strategies (Table 1, developed in consultation with K. Winemiller and K. Rose); we restricted our selection of population data for comparison with those species included in this list; (*ii*) we developed a set of criteria (Table 2) for each endpoint strategy and applied them to each set of population data selected for possible inclusion in our comparisons; data sets were accepted or rejected depending on whether they met the criteria for one of the endpoint strategies.

Following Winemiller and Rose (1992), we use the presence or absence of parental care as our measure of high or low juvenile survivorship. This is the one parameter in their scheme that is measurable in principle but extremely difficult to estimate quantitatively for fish populations in the field. However, the presence or absence of parental care is relatively easy to determine and provides an intuitively reliable index of juvenile survival. In Table 2, we define "parental care" as investment in offspring after fertilization (Gross and Sargent 1985). From the set of possible types and forms of parental care, we chose only those using nest building and nest/brood defense. This provided us with a precise criterion for deciding whether or not a particular population had parental care. There is little question that nest building and nest defense are energetically costly and have, as their only function, the enhancement of offspring survival.

Measures of fecundity and age at maturity

Winemiller and Rose (1992) used egg number per spawning in their definitions of endpoint strategies. In our comparative analyses, we

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chose to work with ovary weight rather than egg number for several reasons: (*i*) ovary weight measures the direct allocation of energy to reproduction in units that are comparable across species, egg number alone ignores differences in egg size, which can be substantial; (*ii*) accurate estimates are easy to achieve in the field; (*iii*) hence, far more useable estimates of ovary weight are available in the literature, thus providing us with larger sample sizes. Following Danylchuk and Fox (1994), we developed our allometric relationships from data on peak ovary weight, as exhibited by breeding females just prior to and during spawning. For each population selected for inclusion in our data set, we estimated female body weight as the average wet weight (W_{AVE}) of sexually mature females sampled just prior to and during spawning. We estimated ovary weight as the average ovary weight of the females included in our estimate of W_{AVE}. Together, these estimates of peak ovary weight and body weight provide measures of both absolute and relative (to body size) energetic investment in offspring per spawning event.

In addition, we wished to compare *annual* energetic investment in offspring. To include opportunistic strategists in this, we needed to estimate their annual spawning frequency. All other endpoint strategies are believed to spawn once per year, so their single spawning effort and yearly effort are identical (Table 2). Attempts to estimate spawning frequency in fish have met with difficulties and different approaches have been adopted (Nikolsky 1963; Hunter and Goldberg 1980). We used the methods of Hunter and Leong (1981) on those populations with sufficient data for their methods. This approach combines laboratory and field data to estimate the number of spawning events in a year (see Appendix A for details). We used this approach for two reasons: (*i*) most recent research has used this technique and (*ii*) it tends to give higher estimates of spawning frequency than earlier procedures. Hence, its use is consistent with our objective of estimating an upper bound for annual direct investment of energy in reproduction.

We estimated age at maturity (Age_{MAT}) as the age at which 50% of the female population became mature. Estimates of female body weight at 50% maturity (W_{MAT}) were based on the age–weight relationships from the sampled population.

Statistical methods

Allometric relationships were estimated using ordinary least squares regression (OLS) on logarithmically transformed data. Residual plots of raw and transformed data were used to confirm the appropriateness of the logarithmic transform. All analyses were done using OLS instead of major axis, or reduced major axis techniques, because (*i*) it remains the most commonly used analytical technique in allometric studies (see Peters 1983) and (*ii*) measurement precision of our dependent variables is considerably less than that of our independent variable and, following McArdle (1988), this situation legitimizes use of OLS techniques. Following Sprugel (1983), we have made corrections for log–log transformations on the slope estimate. Regression lines were compared using analysis of covariance methods, as outlined in Snedecor and Cochran (1967, chap. 14).

For clarity in the Results section, we will use the following notation for the regression model and its corresponding parameters:

$$\ln(Y) = \ln(A_s) + B_s \ln(W)$$

where Y is the dependent variable (e.g., gonad weight), W is the independent variable (body weight), A_s is the y-intercept of the strategy, s, and B_s is the slope for the strategy, s.

Results

Allometry of ovary weight

We began by examining the energetic investment in eggs for a single spawning event, as measured by peak ovary weight. A log–log regression model for peak ovary weight on body weight fitted the data sets for each strategy relatively well (Fig. 1A). Allometric relationships for opportunistic and equilibrium strategists were not significantly ($p > 0.05$) different from each other ($A_O^{sp} = -2.431$, SE = 0.28; $B_O^{sp} = 1.076$, SE = 0.12; $r^2 = 0.91$; $A_E^{sp} = 2.132$, SE = 0.22; $B_E^{sp} = 0.856$, SE = 0.04; $r^2 = 0.95$). Note that superscript "sp" is used here to emphasize that this comparison is based on a single spawning event. Later, when we consider annual spawning effort, we will emphasize the parameters with the superscript "ann".

Pooling data from both strategies yielded the following relationship: $A_{E+O}^{sp} = -2.156$, SE = 0.17; $B_{E+O}^{sp} = 0.882$, SE = 0.03; $r^2 = 0.95$. The allometric relationship for periodic strategists was significantly different ($p < 0.05$) from the pooled relationship for opportunistic and equilibrium strategists, with a much

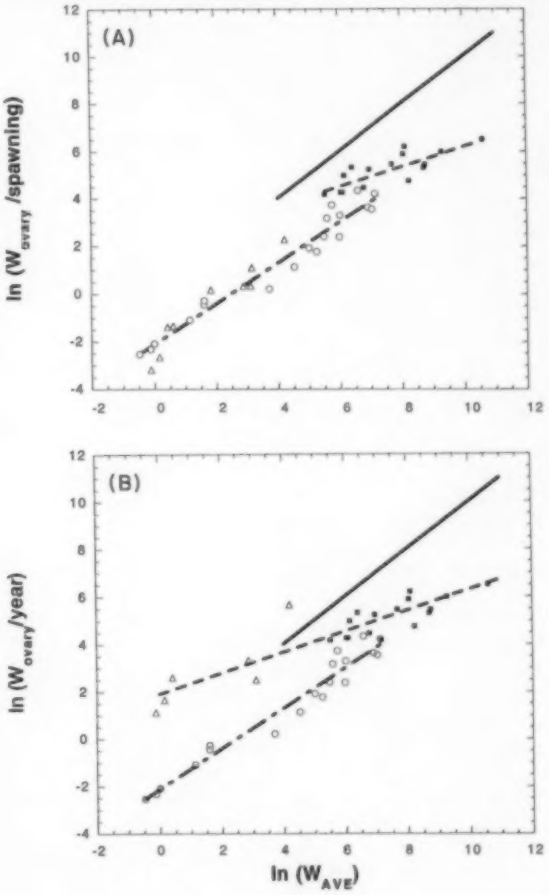

Fig. 1. Natural logarithm of mean peak ovary wet weights plotted against natural logarithm of average female wet weights. The solid curve is the 1:1 curve, where ovary weight is equal to body weight. (A) Data from a single spawning event: equilibrium species (open circles) versus periodic species (solid squares) versus opportunistic species (open triangles). (B) Data for annual spawning effort: extrapolated (annual estimates of ovary production) for opportunistic species (open triangles) versus periodic species (solid squares) versus equilibrium species (open circles). See text for details and Appendix B for references.

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Fig. 2. Two constraint curves for the three endpoint strategies of Winemiller and Rose (1992) and data points from populations not considered one of the three endpoint strategies. See text for details and Appendix B for references.

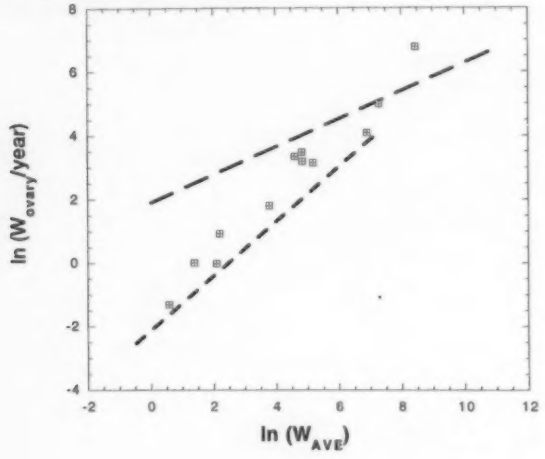
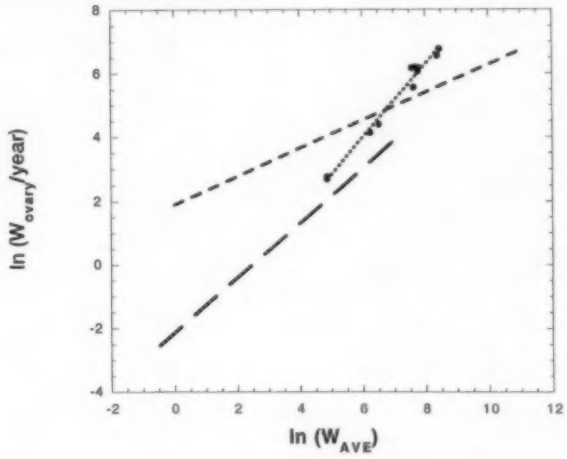


Fig. 3. Two constraint curves for the three endpoint strategies of Winemiller and Rose (1992) and data points from salmon populations (solid circles). Note that the relationship for salmon appears to redefine the upper constraint curve. See text for details and Appendix B for references.



higher intercept value (A_P^{sp} = 1.943, SE = 0.69) and a lower slope value (B_P^{sp} = 0.426, SE = 0.09; r^2 = 0.61).

Next, we examined energetic investment in eggs over an entire year. For equilibrium and periodic strategists, the data were identical to those describing investment in a single spawning event (i.e., $A_E^{sp} = A_E^{ann}$; $B_E^{sp} = B_E^{ann}$; $A_P = A_P^{ann}$; $B_P^{sp} = B_P^{ann}$). For opportunistic strategists, we multiplied our estimate of ovarian investment per spawning by our estimate of the maximum number of spawning events carried out annually. When this was done (Fig. 1B), the data from opportunistic strategists formed a new relationship (A_O^{ann} = 1.505, SE = 0.56; B_O^{ann} = 0.734, SE = 0.23; r^2 = 0.72) that was not significantly different ($p > 0.05$) from that of the periodic strategists. Pooling these two data sets yielded a new relationship (A_{P+O}^{ann} = 1.894, SE = 0.31; B_{P+O}^{ann} = 0.439, SE = 0.04; r^2 = 0.81) that was significantly different ($p < 0.05$) from that exhibited by the equilibrium strategists.

Thus, our analyses of the allometry of ovarian investment by endpoint strategists yielded two consistent relationships that appear to constrain the range for potential ovarian investment as a function of body size. We will refer to the relationship obtained by pooling single spawning investment data from opportunistic and equilibrium strategists as the lower constraint line and the relationship obtained by pooling annual investment data from opportunistic and periodic strategists as the upper constraint line. The behaviour of opportunistic strategists seems to be shaped by both relationships, with investment per spawning set by the lower constraint and annual investment set by the upper constraint.

The generality of this finding was tested by drawing additional data at random from the literature and comparing it with these constraint lines. If the endpoint strategies of the Winemiller–Rose model truly represent bounds on the range of reproductive strategies attainable by fish, then this new set of data should lie between the constraint lines of Fig. 1.

We compared the constraint lines with data from 12 populations (Fig. 2), classified by our algorithm as not representative of any of the three endpoint strategies. Only data from populations with a single annual spawning were included because data on populations with multiple spawning events per year are scarce. Eleven of the 12 points lay within the area bounded by the two constraint lines. The exception was sockeye salmon (*Oncorhynchus nerka*), which lay above the upper constraint. Winemiller and Rose (1992) suggested that salmonids might be exceptions to their categorization.

It seemed significant to us that the one exceptional point came from a population that exhibited a variety of other exceptional reproductive behaviours: semelparous life cycle and extensive prespawning migration. To assess the possibility that similar populations may also be exceptional, and to follow up on Winemiller and Rose's (1992) suggestion that salmonids may form a distinctive group, we gathered peak ovary weight data from other populations belonging to the genera *Oncorhynchus* and *Salmo* (Fig. 3). Again, a log–log regression model for peak ovary weight on body weight fitted the data set relatively well (A_S^{ann} = –2.936, SE = 0.37; B_S^{ann} = 1.153, SE = 0.05; r^2 = 0.98), with both the slope and intercept of the fitted line significantly ($p < 0.05$) different from the slopes and intercepts of both the upper and lower constraint lines.

Allometry of age at maturity

The log–log relationship between age at maturity and body weight was approximately linear with a single regression line, although there was considerable variation (Fig. 4A). We did not find any significant difference in the maturation allometry of the periodic and equilibrium strategies, and statistically the best fit occurred across both strategies (A_{P+E} = 0.2894, SE = 0.13; B_{P+E} = 0.161, SE = 0.02; r^2 = 0.58).

Next, we incorporated age at maturity data from salmon populations because salmon ovarian investment already had proven to be an exception to the original life history model (Fig. 3). We found no significant difference in the maturation allometry of the periodic, equilibrium, and salmon data

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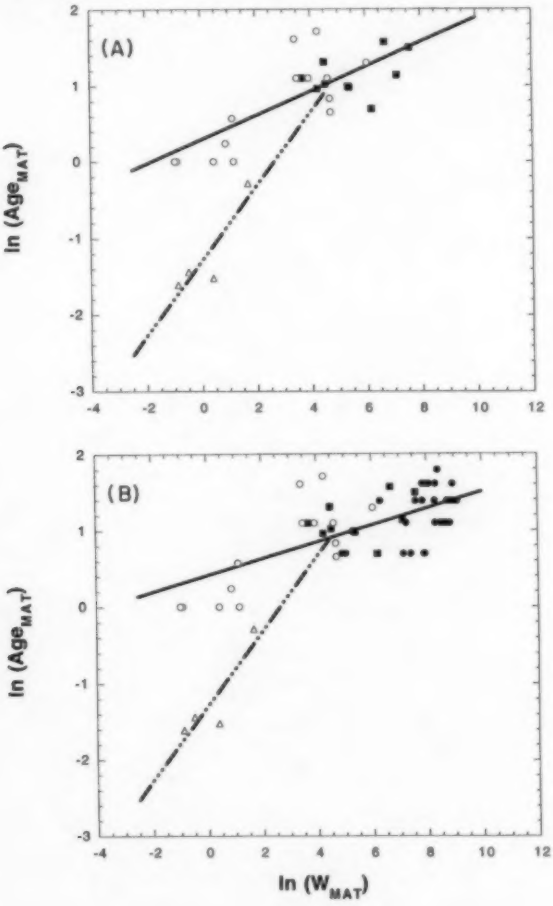
Fig. 4. Natural logarithm of the age of 50% maturity of females plotted against natural logarithm of average female wet weights at age of 50% maturity (W_{MAT}). (A) Periodic species (solid squares), opportunistic species (open triangles), and equilibrium species (open circles). (B) Periodic species (solid squares), opportunistic species (open triangles), equilibrium species (open circles), and salmon species (solid circles). See text for details and Appendix B for references.

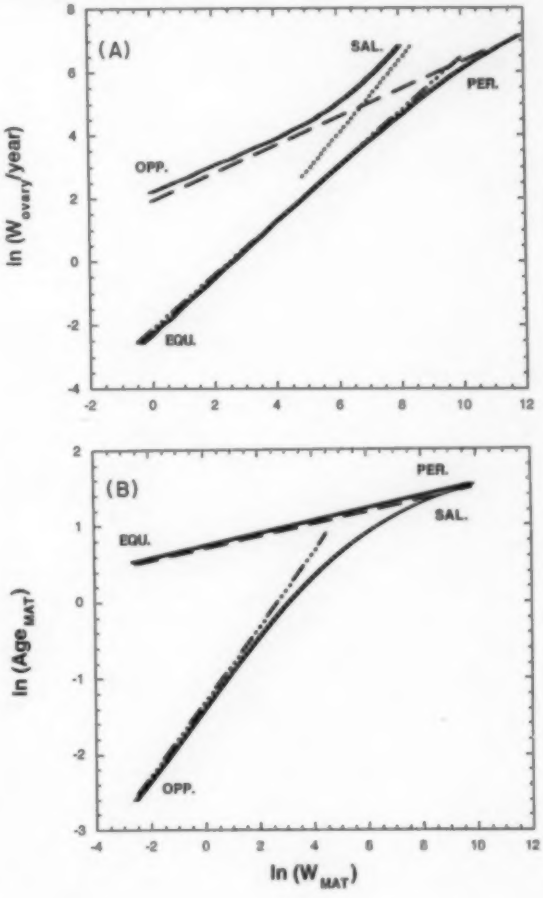


(Fig. 4B), and statistically, the best fit occurred using all three sets of data ($A_{P+E+S} = 0.40$, SE = 0.11; $B_{P+E+S} = 0.11$, SE = 0.01; $r^2 = 0.46$). The data set for opportunistic strategists was small (four points), but all four opportunistic data points fell significantly below the line ($p < 0.04$ for all four points). This early maturation most likely reflects the rapid young-of-the-year growth experienced by opportunistic populations.

Discussion

Allometric scaling of annual ovarian production by North American fish populations appears to be characterized by a pinched rectangular continuum (Fig. 5A), bounded by the three endpoint strategies identified by Winemiller and Rose (1992), plus a fourth strategy, which we will call the salmonic strategy. Moving from the bottom left corner of Fig. 5A clockwise, the rectangle takes as its four corners the smallest equilibrium strategist, the smallest opportunistic strategist, the largest salmonic strategist, and the largest periodic strategist. For a given weight, the range in ovarian production per year, defined by the range in ovary weights between the upper and lower constraint curves in Fig. 5A, reflects the range in reproductive strategies available for a population with that average adult weight, W_{AVE}.

Fig. 5. Representation of the relationships found in the data. (A) Regressions of natural logarithm of mean peak ovary wet weights per year plotted against natural logarithm of average female wet weights (W_{AVE}). The dashed, dashed-dotted, and dotted curves depict the periodic–opportunistic, the equilibrium, and the salmonic relationships, respectively. The solid curves represent the hypothetical smoothed lower and upper constraint curves approximated by these relationships. (B) Regression of natural logarithm of the age of 50% maturity of females plotted against natural logarithm of average female wet weights at age of 50% maturity (W_{MAT}). The dashed and dashed-dotted curves depict the periodic–equilbrium–salmonic and the opportunistic relationships, respectively. The solid curves represent the hypothetical smoothed lower and upper constraint curves approximated by these relationships.



The lower constraint curve, defined by the equilibrium and

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Fig. 6. Schematic of the replacement hypothesis. The solid curve depicts the relationship between total egg biomass produced over an average lifetime versus total biomass recruited into the population from that egg biomass. The total egg biomass (E_{REP}) gives a total recruitment biomass (R_{REP}) that exactly replaces the adult female and mate.

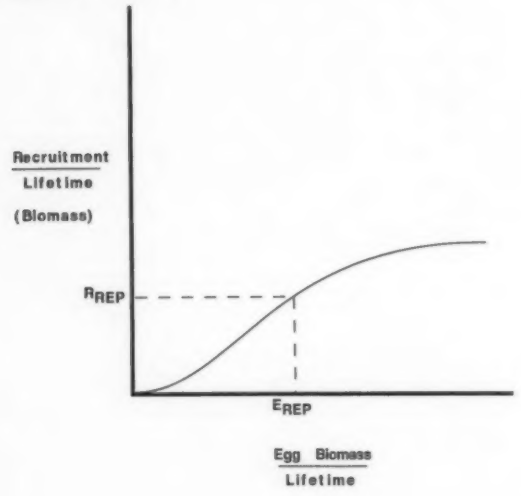
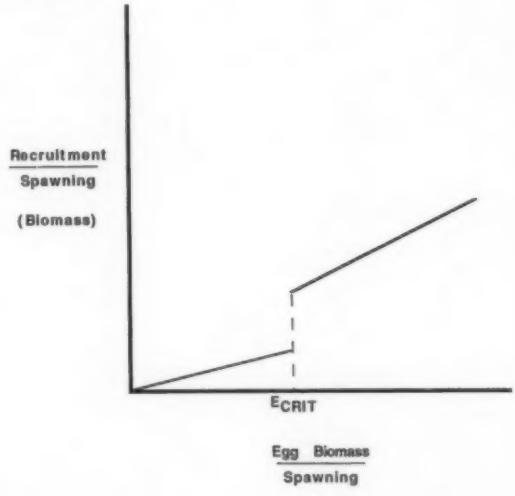


Fig. 7. Schematic of the survivorship hypothesis. The solid curve depicts the relationship between egg biomass produced in a single spawning event versus expected biomass recruited into the population from that single spawning event. Below the egg biomass (E_{CRIT}), recruitment is very low, and above E_{CRIT}, recruitment is relatively high.



periodic strategies, is likely the product of demographic influences. Physical or physiological mechanisms acting on the lower constraint are unlikely because fish populations of identical average female adult weight can produce considerably larger average ovary weight than populations lying on the lower constraint curve (Fig. 5A). At least two different types of demographic constraints might exist: first, the minimum investment in eggs required to permit an individual to exactly replace itself and its mate over the course of an iteroparous *lifetime* (replacement hypothesis), and second, the minimum investment in egg biomass required to insure that survivorship *within a single clutch* remains above some critical value.

The difference in these two hypotheses is best demonstrated graphically. The average recruitment biomass from one individual over a lifetime, as a function of an average individual's total egg biomass over a lifetime, is shown in Fig. 6. In the replacement hypothesis (Fig. 6), there exists a point on this curve that corresponds to the amount of an individual's total egg biomass over a lifetime that gives an average total recruitment biomass, over a lifetime, that exactly replaces the average individual and its mate (depicted by the point (E_{REP}, R_{REP}) in Fig. 6).

The average recruitment biomass that results from a single spawning event, as a function of an average individual's egg biomass in a single spawning event, is shown in Fig. 7. In the survivorship hypothesis (Fig. 7), the curve described by this relationship is discontinuous (or very steep), and below some critical egg biomass (E_{CRIT}), the recruitment biomass is catastrophically low whereas above it, the recruitment biomass is sufficiently high.

Interestingly, the energetic cost of one spawning event by the opportunists lies on the same lower constraint line as the equilibrium (Fig. 1A). This suggests that multiple spawners, within a single event, are held in check by the same lower constraint on ovary weight. Multiple spawners appear to partition their egg biomass as far as the lower constraint allows and no further. This is consistent with the hypothesis that demographic factors determine this constraint. Nevertheless, we are unable to decipher which demographic constraint may be acting.

The upper constraint on annual ovarian production, defined by the opportunistic and salmonic strategists, could be the product of physical factors (i.e., body cavity size), energetic factors (only so much energy can be put into ovary production without causing the death of the female), or demographic factors. However, one observation, that opportunists and salmonic strategists tend to have a short adult life span compared with like-sized equilibrium and periodic strategists, lends support to the energetic constraint hypothesis. This suggests that to reach or surpass the upper constraint in ovary production, an individual must severely compromise postreproductive survival. It will be interesting to see, as more data from salmonic strategists are gathered, if the genus *Salmo* lies below the genus *Oncorhynchus*. The energetic explanation for the upper constraint would predict this because *Oncorhycnhus* populations are typically semelparous whereas *Salmo* populations are iteroparous.

In summary, we suggest that the lower constraint is likely determined by the demographic requirements of population persistence whereas the upper constraint is likely determined by the energetic requirements of individual adult survival.

Note that the size ranges for opportunistic and periodic strategists are disjunct, with the upper bound for opportunistic strategists relatively close to the size (Fig. 1B) where the equality line (body weight = gonad weight) meets the ovarian investment line for periodic strategists. If we assume that the periodic line defines success in certain environments, then multiple, within-year spawning would be obligate for fish living

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in such environments and having body sizes close to, or less than, the size where the periodic line meets the equality line. This could account for the similarity in the allometry of annual investment between opportunistic and periodic strategists. It could also account for the absence of small periodic strategists.

Allometric scaling of maturation age for North American fish is characterized by a single, linear relationship that describes periodic, equilibrium, and salmonic strategists (Fig. 4B). Opportunistic strategists appear to follow a different relationship, maturing much earlier at comparable weights (Fig. 4B). The data suggest a pattern similar to that seen for annual ovarian production (Fig. 5B), with the lower constraint intersecting the upper constraint at a size that matches the lower bounds for both periodic and salmonic strategists.

The relationships summarized in Fig. 5 suggest specific trade-offs as one moves across life history strategies. In Fig. 5A, the strategies associated with the lower constraint curve (equilibrium and periodic) are characterized by relatively low ovarian production and relatively high adult survivorship. The strategies associated with the upper constraint curve (opportunistic and salmonic) are characterized by relatively high ovarian production and relatively low adult survivorship. Hence, when moving vertically from the lower to the upper constraint curve, increased fecundity is traded for reduced adult survivorship across all sizes.

In Fig. 5B, differences are restricted to smaller sizes, where only opportunistic and equilibrium strategists are represented. The lower constraint curve is defined by opportunistic strategists, with their rapid juvenile growth (i.e., see Fig. 4B where time to maturity for opportunistic strategists is clearly much shorter than time to maturity for like-sized equilibrium strategists) and low juvenile survivorship (i.e., absence of parental care). The upper constraint curve is defined by equilibrium strategists, with their lower juvenile growth rates and higher juvenile survivorship (i.e., presence of parental care). Hence, when moving vertically from the lower to the upper constraint curve, increased juvenile growth rate is traded for decreased juvenile survivorship.

If we accept the hypothesis that the upper constraint curve for ovarian investment is energetically imposed, we can use it to estimate the maximum number of spawning events possible for an opportunistic strategist. Let SB_{scope} be the maximum number of spawning events per year for an opportunistic strategist. For a female opportunistic strategist of weight W:

$$SB_{scope} = PRE/RE^{sp}_{ovary}$$

where PRE is potential reproductive effort and RE^{sp}_{ovary} is effort devoted to ovarian investment in a single spawning event. If the upper constraint curve for ovarian investment is energetically imposed, then it is reasonable to assume that it provides an estimate of PRE. Therefore, for a female opportunistic strategist of weight W:

$$SB_{scope} = PRE/RE^{sp}_{ovary} = 55.7W^{-0.443}.$$

Thus, a 10-g fish, adopting the opportunistic strategy with an adult life span of 1 year, should spawn roughly 20 times whereas a 100-g fish with a 1-year adult life span should only be capable of spawning seven times.

Although our study is preliminary, it has shown that differences in life history strategies are reflected in differences in the allometry of some life history attributes. Further work will sharpen the estimates of allometric constraints that contain strategies, as well as identify life history attributes with allometric relationships that are invariant across strategies. Differences in strategy-specific energetics may be more fully understood once sufficient data accumulate to make strategy-specific comparisons of the allometry of consumption rates and metabolic rates.

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Appendix A

All bodily dry weights were converted to wet weights by the following (Clarke 1987):

$$\text{Wet weights} = 3.704 \cdot \text{dry weights}.$$

Calculations of spawning frequency were from Hunter and Leong (1981):

t = spawning period

$f(t)$ = percentage of female population spawning as a function of time (t)

$$\text{Total seasonal spawning events} = \int^{T} f(t)\,dt.$$

Applying this to the data, we made the following rough estimates: bay anchovy = 54.0 (Luo and Musick 1991, previously calculated by author of cited paper); Brazilian sardine = 35.0 (Isaac-Nahum et al. 1988); northern anchovy = 20.0 (Hunter and Leong 1981, previously calculated by author of cited paper); northern anchovy = 8.75 (Hunter and Goldberg 1980); Hawaiian anchovy = 75.0 (Clarke 1987).

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Appendix B

Table B1. Data sources for Fig. 1.

Reference	Species
Blumer 1985	*Ictalurus nebulosus*
Buckley et al. 1991	*Pseudopleuronectes americanus*
Burr 1977	*Lepomis symmetricus*
Burr and Mayden 1982	*Noturus miurus*
Clarke 1987	*Encrasicholina purpurea*
Coates 1988	*Arius solidus*
Coates 1991	*Arius velutin*
Connover 1985	*Menidia*
Dadzie and Aloo 1990	*Micropterus salmoides*
Deacon and Keast 1987	*Lepomis gibbosus*
Etchevers 1978	*Arius spixii*
Finucane et al. 1986	*Scomberomorus cavalla*
Frost and Kipling 1968	*Esox lucius*
Gaigher 1984	*Labeo umbratus*
Harvey and Fortin 1982	*Ictallurus nebulosus*
Hunter and Goldberg 1980	*Engraulis mordax*
Hunter and Leong 1981	*Engraulis mordax*
Isaac-Nahum et al. 1988	*Sardinella brasilensi*
Jones 1974	*Scophthalmus maximus*
Kelley 1962	*Micropterus salmoides*
Kipling and Frost 1969	*Esox lucius*
Laroche and Richardson 1980	*Engraulis mordax*
Luo and Musick 1991	*Anchoa mitchilli*
Macereth 1995	*Micropterus dolomieu*
Mann 1976	*Squalius cephalus*
Mayden and Burr 1981	*Noturus exilis*
Munkittrick and Dixon 1988	*Catostomus commersoni*
Ogutu-Ohwayo 1988	*Lates niloticus*
Olsen and Rulifson 1992	*Morone saxatilis*
Page 1975	*Etheostoma kennicotti*
Page and Burr 1976	*Etheostoma smithi*
Pantulu 1963	*Osteogeneiosus militaris*
Rimmer 1985	*Arius graeffei*
Sinnott and Ringler 1987	*Ictalurus nebulosus*
Treasurer 1981	*Perca fluviatilis*
Weber and Les 1982	*Perca flavescens*
Zastrow et al. 1991	*Anchoa mitchilli*

Table B2. Data sources for Fig. 2.

Reference	Species
Eldridge et al. 1991	*Sebastes flavidus*
Gilhousen 1980	*Oncorhynchus nerka*
Herrera et al. 1988	*Barbus sclateri*
Jester and Suminski 1982	*Cyprinodon tularosa*
Mahon 1977	*Noturus gyrinus*
Mann 1973	*Rutilus rutilus*
Mori 1990	*Gasterosteus aculeatus*
Papageoriou 1979	*Rutulis rutilus*
Rabin and Barnhart 1977	*Clupea pallasi*
Ruple et al. 1984	*Etheostoma swani*
Waiwood and Buzeta 1989	*Melanogrammus aeglefinus*

Table B3. Data sources for Fig. 3.

Reference	Species
Gilhousen 1980	*Oncorhynchus nerka*
Jonsson et al. 1991	*Salmo salar*
Lobon-Cervia et al. 1986	*Salmo trutta*
Morrison 1984	*Oncorhynchus kisutch*
Murray et al. 1989	*Oncorhynchus nerka* (kokanee)

Table B4. Data sources for Fig. 4.

Reference	Species
Beacham 1982	*Pseudopleuronectes americanus*
Burr 1977	*Lepomis symmetricus*
Burr and Mayden 1982	*Noturus miurus*
Conand 1993	*Atherinomorus lacunosus*
Deacon and Keast 1987	*Lepomis gibbosus*
DeMartini and Anderson 1980	*Oxylebius pictus*
Elliot 1985	*Salmo trutta*
Etchevers 1978	*Arius spixii*
Gray et al. 1981	*Oncorhynchus kisutch*
Harvey and Fortin 1982	*Ictallurus nebulosus*
Jones 1974	*Scophthalmus maximus*
Killick and Clemens 1963	*Oncorhynchus nerka*
Kipling and Frost 1969	*Esox lucius*
Leary et al. 1975	*Stolephorus purpureus*
Luo and Musick 1991	*Anchoa mitchilli*
Mahon 1977	*Noturus gyrinus*
Mayden and Burr 1981	*Noturus exilis*
Munkittrick and Dixon 1988	*Catostomus commersoni*
Olsen and Rulifson 1992	*Morone saxatilis*
Page 1975	*Etheostoma kennicotti*
Page and Burr 1976	*Etheostoma smithi*
Pantulu 1963	*Osteogeneiosus militaris*
Quinn and Unwin 1993	*Oncorhynchus tshawytscha*
Ricker 1980	*Oncorhynchus keta*
Rogers 1987	*Oncorhynchus nerka*
Scofield 1931	*Morone saxatilis*
Stearns 1983	*Gambusia* sp.
Treasurer 1981	*Perca fluviatilis*
Weber and Les 1982	*Perca flavescens*
Webster 1954	*Micropterus dolomieu*

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Land–water linkages: influences of riparian deforestation on lake thermocline depth and possible consequences for cold stenotherms

Robert France

Abstract: The purpose of the present study was to determine if riparian deforestation would expose lake surfaces to stronger winds and therefore bring about deepening of thermoclines and resulting habitat losses for cold stenotherms such as lake trout (*Salvelinus namaycush*). Removal of protective riparian trees through wind blowdown and two wildfires was found to triple the overwater windspeeds and produce thermocline deepening in two lakes at the Experimental Lakes Area. A survey of thermal stratification patterns in 63 northwestern Ontario lakes showed that lakes around which riparian trees had been removed a decade before through either clearcutting or by a wildfire were found to have thermocline depths over 2 m deeper per unit fetch length compared with lakes surrounded by mature forests. Riparian tree removal will therefore exacerbate hypolimnion habitat losses for cold stenotherms that have already been documented to be occurring as a result of lake acidification, eutrophication, and climate warming.

Résumé : La présente étude avait pour but de déterminer si le déboisement riverain expose les surfaces des lacs à des vents plus forts qui ont pour effet de déplacer les thermoclines à une plus grande profondeur, entraînant ainsi la perte d'habitat pour les sténothermes d'eaux froides comme le touladi (*Salvelinus namaycush*). On a constaté que l'élimination des arbres protecteurs sur la rive par l'action du vent (chablis) et deux feux naturels triplait la vitesse du vent au-dessus de l'eau et déplaçait les thermoclines à une plus grande profondeur dans deux lacs de la Région des lacs expérimentaux. Un relevé des conditions de stratification thermique dans 63 lacs du nord-ouest de l'Ontario a révélé que les lacs dont les rives ont été dégagées des arbres 10 ans plus tôt, soit par coupe à blanc soit par suite d'un feu de forêt, avaient des thermoclines qui étaient plus profondes (plus de 2 m par unité de longueur de course) que celles des lacs entourés d'une forêt mûre. Ainsi, l'enlèvement des arbres riverains aura pour effet d'exacerber la perte d'habitat pour les sténothermes d'eaux froides dans l'hypolimnion, perte que l'on observe déjà par suite de l'acidification des lacs, de l'eutrophisation et du réchauffement de la planète.
[Traduit par la Rédaction]

"Wind over lake: the image of inner truth"
- the *I Ching* quoted in Backas (1992)

Temperature is a fundamental biological determinant (e.g., Tracy and Christian 1986; France 1991 and references therein) that regulates microhabitat selection (e.g., Spotila et al. 1989). As a result, patterns of temperature stratification in lakes segregate species into thermal habitats that best suit their metabolic requirements (e.g., Magnuson et al. 1979; Christie and Regier 1988). Because the thermocline separates hypolimnetic waters from surface heat sources, cold stenotherms occupy deeper regions during the summer (e.g., Brandt et al. 1980; Crowder and Magnuson 1982). For such species, individual health and population size may be determined by habitat limitations in late summer when the volume of cold water is at a minimum (e.g., Evans et al. 1990; Schofield et al. 1993). Therefore, if any additional anthropogenic stresses reduce the already diminished volume of this essential habitat for cold stenotherms, population reductions and extirpations may result (Coutant 1987).

The purpose of the present study was to investigate the role played by surrounding riparian forests in modifying patterns of wind-induced mixing in Canadian Shield lakes. My hypothesis was that riparian deforestation would expose lake surfaces to stronger winds whose effect could be measured by a deepening of thermocline depths, and thus by inference, cause losses of cold stenothermal habitats. Evidence supporting such a supposition is limited to two studies. Logging of the catchment around a small boreal lake in Finland was thought to increase the mixing depth in 1 year through increased wind action caused by removal of large protecting trees (Rask et al. 1993). A wildfire that burned the catchment of a lake was believed by Schindler et al. (1990) to have contributed to a deepening of the thermocline in a small lake in northwestern Ontario, Canada. My objective in this study was to determine if such results, rather than being particular to these two lakes, instead represent a general response of lakes exposed to riparian deforestation.

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Methods

Reanalysis of data from the Experimental Lakes Area

Data on overwater windspeeds were obtained from an unpublished undergraduate thesis (Solinske 1982) conducted on three lakes in the Experimental Lakes Area (ELA) of northwestern Ontario. These measurements are some of the few that exist (see also Schindler 1971) for small Canadian Shield lakes. Three anemometers, one for each of Lakes 470 (L470), L223, and L239, were situated on floating rafts placed in the middle of each lake so windruns from all compass directions

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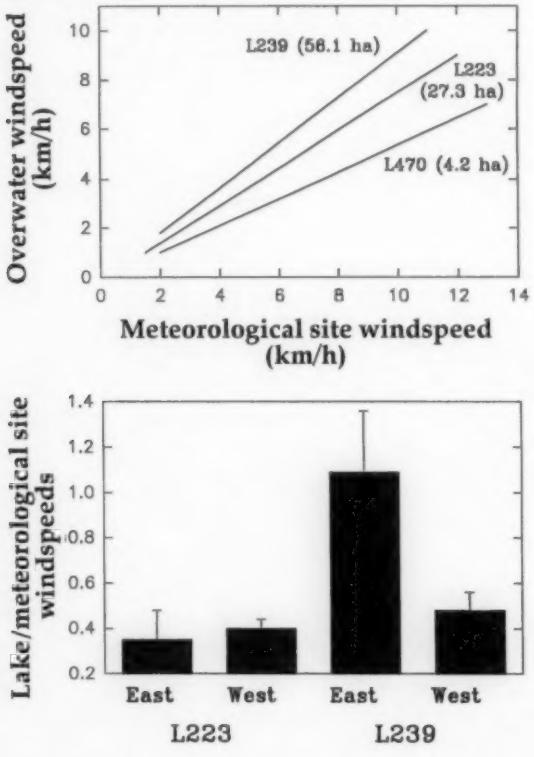
Fig. 1. Upper panel: comparisons between overwater windspeed measured on three boreal lakes of different size and at the meteorological site at the ELA during summer 1981 (reanalyzed data from unpublished thesis of Solinske 1982). Lower panel: mean ratios (±SD) of easterly or westerly windspeeds measured over two ELA lakes during a 2-week period in 1981 to windspeeds at the meteorological site measured at the same time (reanalyzed data from Solinske 1982, see text). L223 is completely surrounded by an intact riparian forest whereas L239 is exposed to winds from the east as a result of a blowdown and forest fire along its eastern riparian shore.



could be recorded. The instruments were situated with wind cups 1.3 m above the water surface so that winds could be monitored without major disturbances created by surface roughness. Data were collected between July 6 and August 24, 1981, and compared with similar measurements made at a meteorological site located 366 m west of L239 at an elevation of 43 m above the lake level (Beaty 1990). Also, for a 2-week period, windspeeds were measured for different directions over L223 and L239. Such land-to-water comparisons are the established procedure (Richards et al. 1966; Phillips and Irbe 1978) and have the effect of lumping all the various influences that cause the winds over water to vary from winds overland (Solinske 1982), i.e., the difference in frictional effect between land and water, differences in atmospheric stability created by air–water temperature differences, and lengths of overwater fetch.

Data on temperature profiles for 1984 and 1985 (Lyng and Cruikshank 1985; Cruikshank 1986) were added to previous information extending back to 1969 (Cruikshank 1984) to examine the relationship between the length of fetch (i.e., the distance in which wind can blow across a water surface) and the average interannual late-summer (July 25 – August 25) thermocline depth for an empirical synthesis of data from 26 ELA lakes. Data for L239 and L240, half of whose riparian shorelines had been denuded due to a blowdown and two wildfires (Schindler et al. 1980, 1990), were not included in this synthesis.

New synoptic survey

Between July 25 and August 25, 1994, I measured temperature profiles in an additional 63 lakes situated within 50–150 km of ELA in northwestern Ontario. As in the previous ELA studies, planar thermocline depth was later calculated as the point of the maximum rate of temperature change (Hutchinson 1957). These data were logarithmically transformed as in Cruikshank (1984). From topographic maps, fetch was measured as the longest straight axis of the lake where winds can blow uninterrupted by landforms. These data were logarithmically transformed as in Hanna (1990). The riparian forests around 10 of the surveyed lakes had been completely clearcut to the water's edge 9–11 years previously (France et al. 1996). For 23 of the surveyed lakes, riparian forests had been completely destroyed in 1980 as part of a massive forest fire (>100 000 ha in extent) that burnt all the way to L239 in ELA. The remaining 30 lakes were surrounded by undisturbed riparian forests and were sampled to establish 1994 references to compare with the more extensive data existing for the 26 different lakes sampled from 1969 to 1985 at ELA.

Mature trees in the shoreline riparian forests around the undisturbed reference lakes (>75-year-old black spruce (*Picea marina*), jack pine (*Pinus banksiana*), and eastern white cedar (*Thuja occidentalis*)) ranged in size from about 8 to 31 m in height depending on surface topography and inshore distance. In contrast, the secondary regrowth on the logged shorelines (9- to 11-year-old trembling aspen (*Populus tremuloides*) and white birch (*Betula papryifera*)) ranged from 0 to 8 m in height. Shoreline trees around lakes located in the massive forest burn area were unmeasured, but as the fire was 13 years old, they were judged to be only slightly larger in size than those present on the clearcut shorelines.

Results and discussion

Influence of fetch on thermocline depth

Overwater windspeeds in relation to data from the nearby meteorological site increased with surface area for three ELA lakes (Fig. 1, upper panel, data from Solinske 1982). Spigel and Imberger (1980) outlined two processes by which the epilimnion is thickened by wind action: (*i*) wind moving across lake surfaces creates a stirring action resulting in a downward forced turbulence and (*ii*) in larger lakes, the turbulence created at the base of the metalimnion results from velocity shearing associated with movement of seiches between warm, less dense metalimnetic and cold, denser hypolimnetic waters. Therefore, because surface wind waves are strongly fetch dependent for most lakes, wind-induced mixing will be greater in larger lakes. Consequently, thermocline depth can be empirically related to fetch length for lakes at ELA in northwestern Ontario (Schindler 1971; Cruikshank 1984; Fig. 2, upper panel), as has been found for lakes located elsewhere (Arai 1981; Shuter et al. 1983; Patalas 1984; Gorham and Boyce 1989; Hanna 1990). Among the 30 forested lakes sampled in 1994, fetch was found to be as good a predictor ($R^2 = 0.97$) of thermocline depth as in the forested ELA lakes sampled previously ($R^2 = 0.85$).

Influence of riparian forests on lake thermocline depth

Hutchinson (1957) proposed that "in theory the degree of exposure or shelteredness should be expected to play a part in determining the thickness of the epilimnion." Data from Solinske

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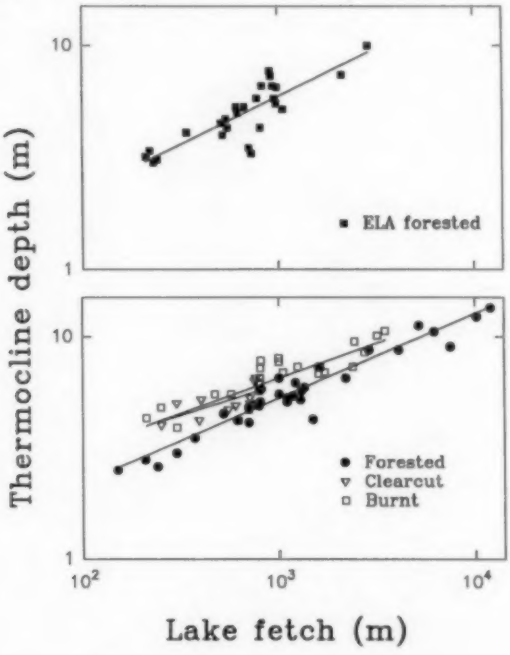
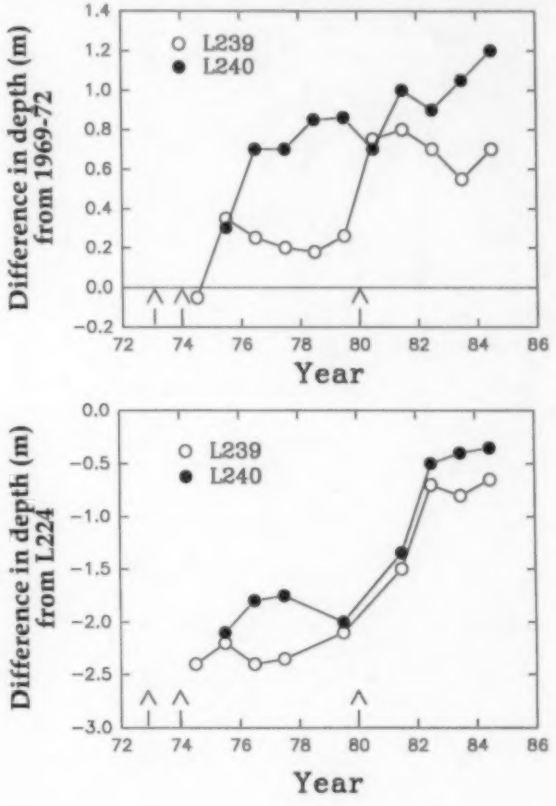
Fig. 2. Relatonship between length of lake fetch and late-summer thermocline depth for (upper panel) 26 ELA lakes sampled during 1969–1985 with forested riparian shores ($y = -0.50 + 0.42x$, $R^2 = 0.85$) and for (lower panel) 63 different northwestern Ontario lakes sampled in 1994 with forested ($y = -0.41 + 0.38x$, $R^2 = 0.97$), clearcut ($y = -0.03 + 0.27x$, $R^2 = 0.72$), and burnt ($y = -0.13 + 0.31x$, $R^2 = 0.86$) riparian shores.



(1982) show that forest cover can indeed have an influence on wind velocities measured over ELA lake surfaces. For L223, which is completely surrounded by an undisturbed riparian forest, originating wind direction had no influence on overwater windspeeds expressed as ratios to meteorological site windspeeds (Fig. 1, lower panel). In such a situation, the forested riparian terrain reduces the velocity of horizontally moving air masses. A major blowdown in 1973 and severe forest fires in 1974 and again in 1980 demolished the forest along the eastern side of L239, leaving barren hills (Schindler et al. 1980, 1990). The highest wind velocities over this lake originated from the east (Fig. 1, lower panel), presumably due to reduced wind resistances (Solinske 1982). Riparian tree removal therefore had the effect of increasing the exposure of L239 to wind energy, a result that, considering the demonstrated importance of fetch to thermocline depth (Fig. 2, upper panel), might be expected to have altered the pattern of thermal stratification.

The average late-summer (i.e., July 25 – August 25) thermocline depths in L239 and adjacent L240 (which had also lost a major portion of its insulating riparian forest due to the same blowdown and fires) were found to increase in the years following forest disturbance (Schindler et al. 1990; Fig. 3, upper panel). To account for long-term trends due to factors other than deforestation, results from L239 and L240 can be compared with data from L224, which escaped the effects of the blowdown and fires. Thermocline depths for L239 and L240 were originally about 2 m less than that in L224 in the mid-

Fig. 3. Changes in late-summer thermocline depths in L239 and L240 in the ELA following blowdown (1973) and burning (1974 and 1980) of riparian forests along their eastern shorelines (arrows) compared with (upper panel) predisturbance (1969–1972) values and (lower panel) values in nearby and completely forested L224.



1970s, but deepened over time toward that in L224, becoming only a 0.5 m less than that of the reference lake by the mid-1980s (Fig. 3, lower panel).

Temporal studies of thermal stratification data for these two ELA lakes (see also independent and different analysis in Schindler et al. 1990 for L239) that had lost their fringing riparian forests due to blowdown and wildfires therefore support similar observations of Rask et al. (1993) for a single Swedish lake whose watershed had been logged. The next step was to see if these findings were particular to just these few individual basins or were representative of a more general response of small boreal lakes to riparian forest clearance.

Residual differences between the lakes sampled in 1994 and the general interannual regression equation for forested ELA lakes ranged from –4 (shallower) to 5 m (deeper), centered about a mode of 0 (Fig. 4). Residual differences in relation to the general interannual ELA regression averaged 2.4 m deeper in thermocline depth for burnt and clearcut lakes (Fig. 4). Regression equations for burnt and clearcut lakes were similar and significantly different (paired ANCOVA tests, p's < 0.05) from that for lakes with forested shorelines. Only two burnt lakes had thermoclines as shallow as predicted from the regression line developed for the forested lakes

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Fig. 4. Frequency distribution of residual differences between thermocline depths measured in forested, burnt, and clearcut northwestern Ontario lakes sampled in 1994 (from Fig. 2, lower panel) and those predicted from the interannual ELA regression equation (from Fig. 2, upper panel).

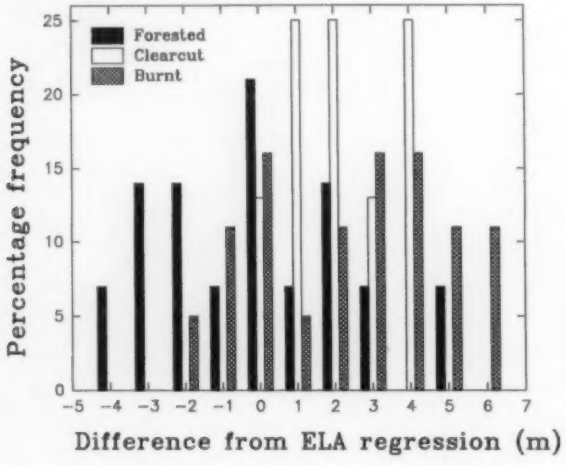
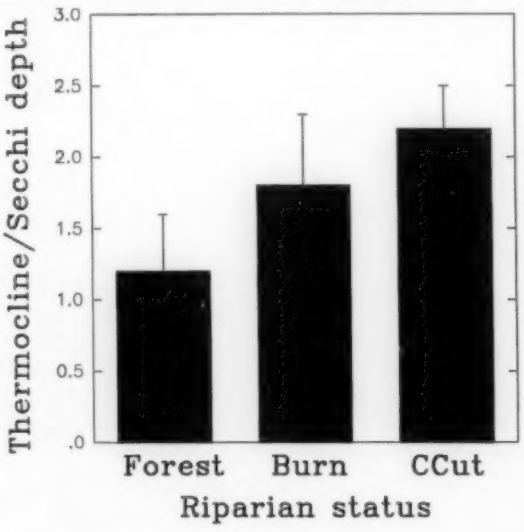


Fig. 5. Comparisons of ratios (±SD) between thermocline and Secchi depths for northwestern Ontario lakes surrounded by intact (Forest), burnt (Burn), and clearcut (CCut) riparian forests.



(Fig. 2, lower panel). Also, as expected, regression lines for the three groups of lakes converged with increasing lake size (Fig. 2, lower panel), suggesting that the insulating role of riparian trees in impeding wind movement may be one of diminishing importance for progressively larger lakes.

In small lakes, water clarity, through controlling the depth of light penetration and extent of solar radiative heating, may also have a modifying role on thermocline depths set by fetch-related wind mixing (Mazumder and Taylor 1994) and therefore thickness of hypolimnia (Teleki and Herskowitz 1986). Although in some situations, these influences of water clarity may be related to algal biomass (Mazumder 1990; Mazumder et al. 1990), in Canadian Shield lakes, colour is often the primary determinant (e.g., Schindler 1971; Dillon et al. 1986; R. France, unpublished data). Clearcut and burnt lakes in this study region of northwestern Ontario have significantly higher colour values, measured as dissolved organic carbon concentrations, and therefore significantly lower water clarities, measured by Secchi depths, than those of forested lakes (R. France, unpublished data). One would therefore expect such lakes to exhibit shallower thermocline depths due to a more rapid heat absorbance closer to the water surface. The fact that the opposite occurred (Fig. 5) indicates the overwhelming dominance of the surrounding riparian forests in modifying the patterns of wind-induced mixing in these small boreal lakes.

Consequences of habitat loss for cold stenotherms

Habitat loss of cold, well-oxygenated hypolimnetic water is widely suspected among fishery biologists to be the major cause of declining lake trout (*Salvelinus namaycush*) stocks in Ontario (Evans et al. 1990; Olver et al. 1991). For example, MacLean et al. (1990) determined that reproduction of lake trout was positively correlated with the depth range and volume of the late summer hypolimnion. Therefore, the demonstration here that thermoclines deepen as a result of riparian deforestation is a further stress on lake trout populations, additional to other habitat compressions by anthropogenic agents such as acidification, eutrophication, and climate warming, as briefly discussed below.

Varied physical–chemical processes occurring within the epilimnion as a result of anthropogenic lake acidification enhance water clarity (e.g., Yan 1983; Shearer et al. 1987), which in turn increases thermocline depth (Effler and Owens 1985) and reduces potential trout habitats (Schofield et al. 1993). Such a development may have contributed to the extirpation of lake trout that has been estimated (Beggs et al. 1985) to have occurred in about 3% of all Ontario lakes.

As a result of nutrient additions from cottage development (Hutchinson et al. 1991), lake productivities have increased, promoting elevated rates of hypolimnetic metabolism and consequently decreased oxygen concentrations (Cornett and Rigler 1980). This shrinkage of hypolimnetic habitat was thought to be a major factor in causing reproductive failures in one quarter of the lake trout populations surveyed in eastern and central Ontario (MacLean et al. 1990).

The predominance of small lake basins of limited depth in northwestern Ontario means that 22% of the lake trout populations located there can be categorized as highly susceptible to extirpation on the basis of lake thermal and oxygen regimes (Ryan and Marshall 1994). The possibility of thermocline deepening in lakes in this region as a result of climate warming (Schindler et al. 1990) may also have detrimentally affected these lake trout populations by reducing the extent of cold, oxygenated habitats (Ryan and Marshall 1994). These problems are further exacerbated because, coincident to rising regional atmospheric and lake temperatures, the incidence of major storm events has increased markedly since the 1950s across Canada (Jardine 1994) as reflected by a doubling of windspeeds measured at the ELA meteorological station between 1970 and 1988 (Schindler et al. 1990).

Cannibalism is an important determinant of lake trout

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recruitment, segregating juveniles from adults to deeper parts of the hypolimnion (Evans et al. 1990). Compression of the thermally available habitat, as through riparian deforestation, for example, therefore concentrates lake trout, increasing interaction and competition as well as the potential for cannibalism.

Empirical estimates suggest that in half of Ontario lakes, less than 6% of the total lake volume is suitable for juvenile lake trout, and in one fifth of the lakes, only 1% of the lake volume is available for such nursery development (Evans et al. 1990). Because most of the lakes containing lake trout in northwestern Ontario are already near the minimum depth necessary for sustaining viable populations (about 28 m), any changes in hypolimnion volume may exacerbate the potential for regional extinctions (Ryan and Marshall 1994). As a result, thermocline deepening produced by riparian deforestation, although of a magnitude of only several metres in extent, might still impair lake trout recruitment and population survival. If hypolimnia are compressed in thickness to less than 3 m, both oxygen concentrations and trout carrying capacities decline markedly (Teleki and Herskowitz 1986).

Habitat compression is not only a concern for lake trout. Other cold stenotherms such as deepwater sculpin (*Myoxocephalis quadricornis*), amphipods (*Diporeia hoyi*), and opposum shrimp (*Mysis relicta*) are also dependent on cold, deepwater refugia during the summer (Dadswell 1974).

Implications for riparian forest management

As a result of the widely recognized negative influences of siltation on salmonid egg survival, Ontario restricts riparian clearcutting around lakes known to contain trout populations (Ontario Ministry of Natural Resources 1988). Over the last two decades, however, there has been a progressive shrinkage in the recommended widths for protective buffer strips around such trout lakes (Ontario Ministry of the Environment 1994). At present, it is possible to remove trees to within 30 m of lakes on riparian shorelines of less than 30% surface slope (Ontario Ministry of Natural Resources 1988, 1991). In Quebec, where actual buffer strip "laws" exist, rather than mere "recommendations" or "guidelines" as is the case in Ontario, it is possible to cut to within 20 m of lakes regardless of either riparian slope or type of fish species present (Québec Ministère des Forêts 1992). Buffer strips are susceptible to blowdown due to being newly exposed to considerable wind energy (e.g., Alexander 1964; Steinblums et al. 1984; Stephenson 1988). Whether such buffer strips will be of sufficient width to protect pelagic zones from increased wind energy through the period of backshore forest regrowth is unknown, and worthy of future investigation.

The present study measured a doubling of thermocline depth per unit Secchi depth a decade after the complete logging of riparian forests around 10 lakes. The average height of sapling regrowth on these shorelines was 2 m, enough to substantially reduce wind energy (e.g., Moen 1967; Capel 1988; Johnson and Beck 1988). It is possible, therefore, that lake mixing depths may have been even deeper immediately following riparian deforestation. For example, the greatest increases in thermocline depth in L239 and L240 occurred during or immediately following tree blowdown and burning. Easterly windspeeds over L239 1 year after removal of the last of the riparian trees during the massive wildfire of 1980 were almost three times greater than those originating from the forested western shore. Almost a century is required for forests to reach maturity in this region of northwestern Ontario. The protection offered by riparian trees with respect to the influences of wind-induced lake mixing will therefore undergo a gradual process of recovery to predisturbance levels. Whether lake trout populations and other cold stenotherms can adapt to such prolonged periods of recurring habitat compression following the initial, most severe effect is an important management issue necessitating predictive modelling along the lines of that initiated by Ryan and Marshall (1994).

Note added in proof

Two recent published analyses of ELA data give credence to the conclusions of the present study. Schindler et al. (1996) state: "It is difficult to discount entirely the role of increased wind velocities and wind exposures. Surface waves on small ELA lakes became larger after catchments were burned because less protection was afforded by denuded shorelines. The effect was noticeable enough to require that boats at the dock on Lake 239 had to be tied bow outward to prevent swamping when winds were onshore—a procedure that was not necessary in the early 1979s." The data presented here in Fig. 1 (lower panel) provide the empirical support for Schindler et al.'s (1996) anecdote about increased wind at L239 and nearby L240 relative to other unburnt ELA lakes (this paper, Fig. 3 (lower panel), which therefore contributed toward the progressive increases observed in summer thermal capacities of L239 and L240 (Schindler et al. 1996, Fig. 9).

Schindler et al. (1996) continue, however, with the statement: "Nevertheless, the empirical analysis of Fee et al. (1996) indicated that increased wind exposure played a negligible part in thermocline deepening of small ELA lakes." Despite this statement, Fee et al.'s (1996) data do seem to support both Schindler et al.'s (1996) anecdotal evidence as well as the present analysis. Fee et al. (1996) present a convincing case that water transparency plays a major role in regulating epilimnetic mixing depth in small ELA lakes. Further, a comparison of results shown in their Fig. 6 and Table 2 indicates that the mixing depth in L239 was 1.3 times greater per unit water transparency compared with that in L223. Although, of course, some of this difference may be attributable to the fact that L239 experiences greater wind velocities on account of its greater size (this paper, Fig. 1 (upper panel), Fee et al.'s (1996) findings support my regional analysis shown in Fig. 5 whereby lakes exposed to winds through riparian deforestation do have greater ratios of thermocline to Secchi depth.

Acknowledgements

This work was funded by an NSERC Strategic Grant to study the effects of deforestation on ecotonal land–water coupling. I thank M. Schlaepfer for field assistance, R. Steedman for providing facilities at the OMNR Coldwater Lakes Research Camp, and R. Kushnerik and K. Beaty for supplying A. Solinske's unpublished thesis. Conversations with the late R. Peters on empirical limnological issues in general, and with reference to lake mixing depths in particular, were much appreciated and will be sadly missed.

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Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*)[1]

Vytenis Gotceitas, Sandra Fraser, and Joseph A. Brown

Abstract: Two field surveys were conducted in Newfoundland, Canada: (1) SCUBA surveys at four sites differing in bottom type and the presence/absence of vegetation and (2) beach seining at three sites containing eelgrass (*Zostera marina*) and no-eelgrass locations. Results indicated that eelgrass is used as a nearshore habitat by age 0+ Atlantic cod (*Gadus morhua*). A subsequent laboratory experiment compared the use of patches of bottom substrates (sand, gravel, cobble) and artificial eelgrass (three densities) by age 0+ cod when in the absence and presence of a predator (an age 3+ conspecific). Before exposure to a predator, age 0+ cod associated with sand and gravel. With a predator present, in substrate combinations with cobble, age 0+ cod hid in the interstitial spaces of this substrate or in the patch of eelgrass when stem density was ≥720 stems/m^2. In combinations with no cobble, age 0+ cod hid in the eelgrass regardless of stem density. Latency to capture an age 0+ cod was highest and the total number of age 0+ cod captured lowest in combinations with cobble or the patch of vegetation with 1000 stems/m^2. In the remaining combinations, latency until an age 0+ cod was captured increased with both the presence and density of vegetation.

Résumé : Deux relevés sur le terrain ont été réalisés à Terre-Neuve, Canada : 1) des relevés par plongeurs autonomes dans quatre sites différant par le type de fond et par la présence ou l'absence de végétation et 2) relevé à la seine de rivage dans trois sites contenant et ne contenant pas de zostère marine (*Zostera marina*). Les résultats ont indiqué que la zostère est utilisée comme habitat de littoral par la morue franche (*Gadus morhua*) d'âge 0+. Une expérience de laboratoire subséquente a été réalisée pour comparer l'utilisation des zones de substrats de fond (sable, gravier, galets) et de zostère artificielle (trois densités différentes) par la morue d'âge 0+ en l'absence et en présence d'un prédateur (un congénère d'âge 3+). Avant l'exposition à un prédateur, les morues d'âge 0+ fréquentaient les zones recouvertes de sable et de gravier. Avec la présence du prédateur, dans les combinaisons de substrat contenant des galets, les morues d'âge 0+ se cachaient dans les espaces interstitiels dans ce substrat ou dans les herbiers de zostère lorsque la densité des tiges était ≥ 720 tiges/m^2. La période de latence avant capture des morues d'âge 0+ était la plus longue et le nombre total de morues d'âge 0+ capturées était le plus faible dans les combinaisons contenant des galets ou des zones de végétation ayant une densité de 1 000 tiges/m^2. Dans les autres combinaisons, la période de latence a augmenté en fonction de la présence et de la densité de la végétation.
[Traduit par la Rédaction]

Introduction

Beds of aquatic vegetation appear to play an important role as nursery habitat for a wide variety of marine and freshwater fish species. Along with an abundant food source, vegetated habitats also provide juvenile fishes with protection from predation (Orth et al. 1984; Gotceitas and Colgan 1989). Protection appears to be the result of a significant negative effect on the foraging success of predators with increasing plant stem density, biomass, or complexity (Nelson 1979; Stoner 1982; Gotceitas 1990; Nelson and Bonsdorff 1990; Isaksson et al. 1994). When avoiding predators, prey have been shown to select among patches of vegetation, choosing those that offer safety from predation (Gotceitas and Colgan 1987, 1989).

Following a pelagic egg, larval, and early juvenile stage, age 0+ Atlantic cod (*Gadus morhua*) settle out of the water column and become demersal. Field and laboratory studies have identified bottom substrate type (Lough et al. 1989; Gotceitas and Brown 1993; Tupper and Boutilier 1995*a*, 1995*b*) and the presence of macroalgae (Gjøsæter 1987; Keats et al. 1987; Gotceitas et al. 1995) as important features influencing the distribution of demersal juvenile cod. In contrast, while statements made in various studies suggest that seagrass beds may also be used as a habitat by juvenile cod (Tveite 1984; Støttrup et al. 1994), only recently has a study examined this directly (Tupper and Boutilier 1995*b*). In their study, conducted in St. Margaret's Bay, Nova Scotia, Canada, Tupper and Boutilier (1995*b*) found that young-of-the-year Atlantic cod settled out onto a number of different nearshore habitat types, including seagrass beds. In our study, we conducted two field studies to examine whether juvenile Atlantic cod use eelgrass beds (*Zostera marina*) as a habitat in the nearshore environment of Newfoundland, Canada.

We first examined use of eelgrass by juvenile cod using a SCUBA survey to compare use of eelgrass with that of several other habitat types predicted from laboratory studies (Gotceitas and Brown 1993; Gotceitas et al. 1995) to be important to juvenile cod. This study was conducted on a relatively small spatial scale, sampling several habitat types within a single bay. Based on results from the SCUBA study, we then conducted a beach seine survey to examine use of eelgrass by

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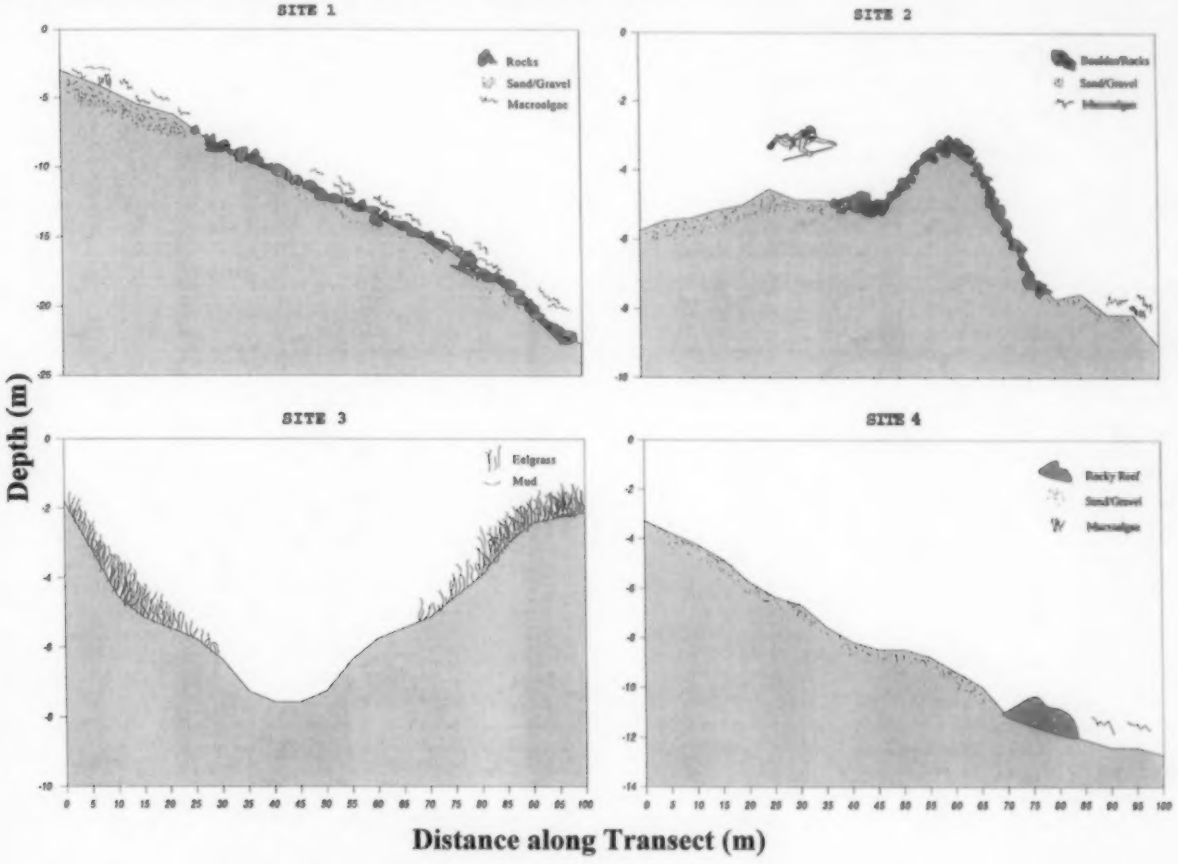
Fig. 1. Cross-sectional profiles of the four SCUBA survey sites in Bull Arm, Trinity Bay, Newfoundland, showing depth and bottom/habitat composition (size of bottom substrates, macroalgae, and eelgrass not drawn to scale).



juvenile cod over a larger geographic area by sampling eelgrass and adjacent no-eelgrass sites in several different bays around Newfoundland.

Various organisms use seagrass beds as a refuge from predation (reviewed in Orth et al. 1984). Therefore, as a follow up to our field studies, we carried out a laboratory experiment to investigate whether eelgrass might be used as a refuge from predation by juvenile cod. Experiments presented age 0+ cod with a choice between safe and unsafe bottom substrates (Gotceitas and Brown 1993) and a patch of artificial eelgrass in the absence and presence of a predator.

Materials and methods

Field studies

Surveys were conducted by SCUBA at four sites in Bull Arm, Trinity Bay, Newfoundland, Canada (47°50′N, 53°53′W). Each site was characterized by the dominant substrate/habitat type present: site 1, rocks/cobbles (particle size = 7–50 cm in diameter) with attached macroalgae (*Chorda tomentosa* and *Agarum cribrosum*); site 2, rocks/cobbles, boulder (particle size >50 cm in diameter), and gravel (particle size = 0.5–1.5 cm in diameter); site 3, eelgrass and mud; site 4, sand (particle size <0.1 mm in diameter), gravel, and a small rocky reef (i.e., bedrock outcropping) (Fig. 1). The habitat types surveyed represent ones commonly found in the nearshore environment around Newfoundland. Sites were selected to allow us to (1) examine if juvenile cod use eelgrass as a habitat, (2) compare the distribution of juvenile cod among a number of different nearshore habitat types, and (3) provide a comparison between habitat use by juvenile cod observed in the field and that suggested from the results of laboratory studies on substrate use (Gotceitas and Brown 1993) and use of macroalgae (Gotceitas et al. 1995).

A permanent transect, 100 m long, running perpendicular to the shoreline was established at each site in June 1993, and all transects were sampled once every 2 weeks from July to December 1993. All four sites were sampled during a 1-day period, between 12:00 and 17:00. Transects consisted of the area between two polypropylene ropes, 2 m apart, threaded through eyelets in the top of metal spikes (65 cm long, 1.5 cm in diameter) that were driven into the bottom at 10-m intervals. Sampling consisted of two divers swimming beside each other along the length of the transect. Each diver recorded (*i*) the number and age of juvenile cod on the transect and (*ii*) habitat type present at the location where fish were observed. Each transect took an average (±1 SE) of 15.2 ± 0.59 min to survey. Age of cod observed was estimated based on previously established age–length relationships for juvenile Atlantic cod in Newfoundland (i.e., age 0+, ≤10 cm standard length (SL); age 1+, 10–20 cm SL; age 2+, 20–30 cm SL; age 3+ and older, >30 cm SL) (Methven and Bajdik 1994; V. Gotceitas, unpublished data).

A preliminary beach seine survey to identify accessible nearshore

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Table 1. Abiotic characteristics of the two sampling locations (i.e., eelgrass and no-eelgrass) at each sampling site in Trinity, Bonavista, and Notre Dame bays, Newfoundland, as recorded at the time of sampling (NA, data not available; see text for details).

Site	Location	Maximum depth (m)	Bottom temperature (°C)			Salinity (ppt)		
			Oct.	Nov.	Dec.	Oct.	Nov.	Dec.
Trinity Bay	Eelgrass	5.3	8.6	5.2	3.0	30.6	31.4	31.1
	No-eelgrass	7.9	6.9	5.5	5.5	30.6	31.1	31.1
Bonavista Bay	Eelgrass	3.9	9.2	6.0	3.0	28.5	29.6	31.3
	No-eelgrass	5.7	9.1	5.6	3.2	28.6	29.6	31.3
Notre Dame Bay	Eelgrass	0.9	6.1	5.1	NA	10.4	19.5	NA
	No-eelgrass	0.9	6.0	NA	NA	8.8	NA	NA

sites that were suitable for our sampling protocol was conducted in September 1994. Subsequently, three sites (Sunnyside in Trinity Bay (47°51′N, 53°54′W), Musgravetown in Bonavista Bay (48°24′N, 53°53′W), and Davidsville in Notre Dame Bay (49°21′N, 54°26′W), Newfoundland, Canada) were sampled over a 1-week period, once a month from October to December 1994. All samples were collected during the day at low tide ±2 h. Two locations (maximum distance between locations = 750 m) were sampled at each of the three sampling sites. Locations were chosen to include one where eelgrass was a dominant feature of the demersal habitat (i.e., >80% bottom cover) and the other without eelgrass. The eelgrass location in Trinity Bay was site 3 from our SCUBA survey the previous year. The substrate at the no-eelgrass location in Trinity Bay was primarily composed of sand, gravel, and pebbles, with some cobble present. In Bonavista Bay, the no-eelgrass location was dominated by a sand/gravel bottom, with some cobble present. At this location, there was also a 3- to 5-m band of rocky bottom with macroalgae on it located 2 m from the shoreline. Finally, the no-eelgrass location in Notre Dame Bay had a primarily sand/gravel bottom. Various abiotic characteristics of each sampling location were also recorded on each sampling day (Table 1).

Samples were collected using a 25-m beach seine (wings and belly 19-mm stretch mesh, codend 9-mm stretch mesh bag; 24.4-m headrope, 26.2-m footrope; aluminum Dan Leno Sticks on each wing were 75 cm long and 25 mm in diameter). The net was deployed from a small (6 m) boat at a distance of 55 m offshore and retrieved by two individuals standing 16 m apart on the shore. The seine was pulled along the bottom and sampled 2 m up into the water column. Qualitative SCUBA observations on the vertical distribution of juvenile cod relative to the bottom, and direct observations behind the seine while in use, indicate that less than 5% of all fish enclosed by the net were either missed or escaped from the net (V. Gotceitas, personal observation). Two consecutive samples were taken at each sampling location, on each sampling date. All fish collected were identified and counted. Juvenile cod were also aged, based on the previously described length–age relationship (see SCUBA survey).

The influence of collection site (i.e., bays), month of collection, whether eelgrass was present or not, and age of cod on the number of juvenile cod captured was examined using an analysis of variance (ANOVA in Proc GLM, SAS Institute 1988). Data were square root transformed to meet the assumptions of the test. Subsequently, multiple *t*-tests (LSMEANS in Proc GLM, SAS Institute 1988) were used to compare catches of juvenile cod among bays within each month, over time within each bay, and between eelgrass and no-eelgrass locations within each bay over the course of the sampling period. Results from these analyses were compared with a *p*-value corrected for the three bays and three months of sampling ($p = 0.05/3 \times 3 = 0.006$, Bonferroni method) and for the three bays, three months of sampling, and two locations sampled within each bay ($p = 0.05/3 \times 3 \times 2 = 0.003$), respectively. Finally, using multiple *t*-tests, we examined catches of juvenile cod from eelgrass versus no-eelgrass sites, within each bay over the course of the study period with respect to the age (i.e., ages 0+ and 1+) of the juvenile cod captured ($p = 0.05/3 \times 3 \times 2 \times 2 = 0.001$).

Laboratory experiment

The age-class of cod used in this experiment was that found to use eelgrass as a habitat in our field investigations. Juvenile, age 0+ (3.5–10.0 cm SL) and larger, age 3+ (30–50 cm SL) cod were collected by the same beach seine used in our beach seine survey. Age 0+ cod were collected during our preliminary beach seine survey (September 1994). Age 3+ cod were collected from various nearshore sites in Trinity Bay. Fish were brought back to the laboratory (Ocean Sciences Centre, Logy Bay, Nfld.) and housed in flow-through tanks (1 × 1 × 0.47 m deep) maintained within a temperature range of 3–10°C. This was done to eliminate possible confounding effects of changing seawater temperature on habitat use by juvenile cod over the course of the experiment (i.e., fall–winter–spring) and in an attempt to conduct our experiments at temperatures similar to those observed in the field at the time of our field studies (Table 1). While in the holding tanks, fish were fed chopped capelin (*Mallotus villosus*).

Experiments were conducted in a flow-through tank (2 × 2 × 0.5 m deep) housed behind a blind with a viewing slit in it to eliminate outside disturbances. The tank was divided into a central experimental area (2.812 m^2) and four predator housing compartments, one located in each corner of the tank. Each predator housing compartment was closed off from the experimental area by a piece of opaque Plexiglas (1 × 0.5 m high), with access for the predator to the experimental area by way of a sliding door (15 × 19 cm high) built into the centre of each compartment. The door to each compartment could be opened and closed by an observer while behind the blind.

Temperature in the experimental tank was maintained at 3–10°C, to match that in the holding tanks, and water depth was kept at 0.4 m. Illumination was provided by four 15-W incandescent light bulbs suspended 1.17 m above the water surface. Lights were centred over the tank, with one bulb located in each corner of a 0.9 × 0.9 m frame. Lights were on a 12 h light : 12 h dark schedule.

Bottom substrates were collected from along the shore. In the laboratory, these substrates were cleaned, dried, and sorted according to size by running them through a series of metal sieves (Tyler Sieves, Canadian Standard Sieve Series). Substrate was divided into three categories based on particle size: sand (<1 mm in diameter), gravel (5–15 mm in diameter), and cobble (70–200 mm along the longest axis). Substrates were chosen to include (1) a size range typically found in the nearshore environment around Newfoundland, (2) a sample of those substrates present at the various sites sampled during our field studies, and (3) bottom types that have been previously shown to offer juvenile cod protection from predation (i.e., cobble) and those that do not (i.e., sand and gravel) (Gotceitas and Brown 1993). Comparing use of eelgrass by age 0+ cod when under the risk of predation with that of safe and unsafe bottom types (see below) that are also present in their natural environment allowed us to both examine the refuge potential of eelgrass and compare laboratory results on habitat use with that observed in our field studies.

Patches of artificial eelgrass were made from lengths (30 cm) of green polypropylene rope (0.4 mm in diameter) attached at one end to a Plexiglas base in a uniform distribution. Attached in this way, individual "stems" floated upright in the water column, while the base sat

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on the tank bottom. Patches of 520, 720, and 1000 stems/m^2 were tested. These densities are within the range observed in the field (V. Gotceitas, personal observation).

Prior to conducting experiments, four of the age 3+ cod previously collected ("predators") were trained to enter the experimental area to feed once the door to their predator housing compartment was opened. Predators were considered ready for use in experiments when they readily (i.e., <5 s) entered the experimental area once the door to their compartment was opened.

Each experimental trial presented a group of five, experimentally naive, age 0+ cod with a choice of three "substrates" in the absence and presence of a predator. Each combination of substrates included two mineral substrates and one density of artificial eelgrass. A total of six combinations were tested. Three combinations presented the juveniles with two unsafe bottom substrates and vegetation (i.e., sand and gravel with 520 stems/m^2 = combination "Sgv520", 720 stems/m^2 = combination "Sgv720", and 1000 stems/m^2 = combination "Sgv1000"). The other three presented a safe (cobble) and unsafe (sand or gravel) bottom type and vegetation (i.e., cobble and sand with 520 stems/m^2 = combination "Csv520" or 720 stems/m^2 = combination "Csv720" and cobble and gravel with 1000 stems/m^2 = combination "Cgv1000"). Location of the three substrate types in the experimental area was assigned at random. Each of the substrates covered one third of the bottom in the experimental area, and each one bordered the other two, with all three meeting in the centre of the experimental area. Each combination of substrates was presented to at least five different groups of age 0+ cod.

Each experimental trial ran over a 2-day period. A group ($n = 5$ fish) of age 0+ cod was introduced into the experimental area at 16:00 the day prior to starting a trial to allow for a period of acclimatization. On day 1 of each trial the distribution of age 0+ cod with respect to the three substrates was recorded (i.e., the number of individuals present on each substrate) at 1-min intervals during three 15-min "observation periods" conducted at 09:00, 12:00, and 16:00. No risk of predation to the age 0+ cod was present during day 1.

On day 2, the distribution of age 0+ cod was again recorded in the absence of any predation risk at 09:00 and 12:00. Immediately following the 12:00 observation period, one of the predators was released into the experimental area and the distribution of both the age 0+ cod and predator was recorded at 1-min intervals over the next 15 min. Following this observation period the predator remained in the experimental area for another 30 min, after which the distribution of both the predator and age 0+ cod was again recorded over a 15-min observation period. Following this second observation period, the predator was returned to its chamber. Latency (minutes) until the first age 0+ cod was captured and the total number of age 0+ cod captured were recorded over the entire period (1 h) that the predator was present. Finally, one last 15-min observation period was conducted at 16:00 on day 2 to record the distribution of age 0+ cod among the substrates following exposure to a predation threat. Which of the four predators was released during any one trial was determined in a semirandom fashion, such that each predator was exposed at least once to each substrate combination.

Data analyses

An estimate of the proportion of time that age 0+ cod spent on each of the three substrates during any one observation period was calculated by summing the counts of fish recorded on that substrate each minute over the 15-min total (i.e., maximum = 5 fish × 15 min for any one substrate during any one observation period) and dividing by the total time available (total time available = sum of the number of fish present at the end of each minute over the 15-min observation period, maximum = 5 fish × 15 min). It was necessary to use the proportion of time available that fish spent on each substrate in order to correct for reductions in the total number of age 0+ cod present between observation periods within any one trial due to losses to predation.

Effects of substrate combination and "predator exposure" (i.e., before exposure to a predator = "BP", during exposure to a predator = "DP", and after exposure to a predator = "AP") on the proportion of time that age 0+ cod spent on each substrate were analysed using multivariate analysis of variance (MANOVA in Proc GLM, SAS Institute 1988). Subsequently, multiple t-tests were used to make univariate pairwise comparisons of substrate use by age 0+ cod across predator exposure conditions within substrate combinations (least squares means in Proc GLM, SAS Institute 1988). Results from the multiple t-tests were compared with a p-value corrected for the three substrates present in each combination and the three predator exposures compared (Bonferroni method, $p = 0.05/3 \times 3 = 0.006$).

Substrate use by age 0+ cod in each substrate combination within each predator exposure condition was compared using chi-square goodness-of-fit test assuming a random distribution among substrates (i.e., use of substrates in accordance to their availability). A similar analysis was done on the predator's use of substrates within each substrate combination. Actual count data (i.e., number of fish observed) were used for these analyses. We also examined whether substrate use by age 0+ cod was independent of that by the predator using multiple contingency tables (Proc Freq, SAS Institute 1988). In substrate combinations where results indicated that substrate use by age 0+ cod was somehow influenced by substrate use by the predator, this was further investigated using lambda association measures (Bishop et al. 1975), where values of lambda/asymptotic standard error (ASE) >2 were taken to indicate a significant increase in the accuracy of predicting substrate use by age 0+ cod if substrate use by the predator was known.

Mean latency until the first age 0+ cod was captured by the predator and mean total number of age 0+ cod captured were compared among substrate combinations using ANOVA (Proc GLM, SAS Institute 1988). Data for number of juveniles captured had to be rank transformed prior to analysis.

Finally, to specifically investigate the effects of artificial eelgrass on latency and number of age 0+ cod captured, data from this experiment were also compared (ANOVA, Proc GLM, SAS Institute 1988) with data collected during an earlier study in which identical bottom mineral substrates were tested with no eelgrass present (Gotceitas and Brown 1993). To satisfy the assumptions of the test, latency data had to be $\log_{10}$ transformed. Data for the number of age 0+ cod captured had to be rank transformed.

Results

Field studies

SCUBA survey

Substrate use by juvenile cod appears to vary with the age of the fish (Fig. 2). All but one of the age 0+ cod observed were found in association with eelgrass. The one other age 0+ fish was recorded over a fine mineral substrate (i.e., mud) within 1–2 m of the eelgrass at site 2 (Fig. 1). In contrast, most of the age 1+ and older cod appeared to prefer a rocky substrate with macroalgae associated with it (Fig. 2). The exceptions were one age 1+ cod that was observed over the sand/gravel substrate at site 4 and one age 2+ cod observed in association with the coarse, boulder/rocks substrate at site 2 (Fig. 1). The pattern of habitat association by age 0+ cod with eelgrass, and older juvenile cod with rocks and macroalgae, was fairly consistent over the 6 months of the study (Fig. 2).

While the rock with macroalgae habitat at site 1 extended from a depth of 9.6 m to the end of the transect (depth = 22.5 m), no cod were observed at a depth of less than 15 m (Table 2). Qualitative observations indicated that this distribution placed fish in colder water, below a thermocline, which

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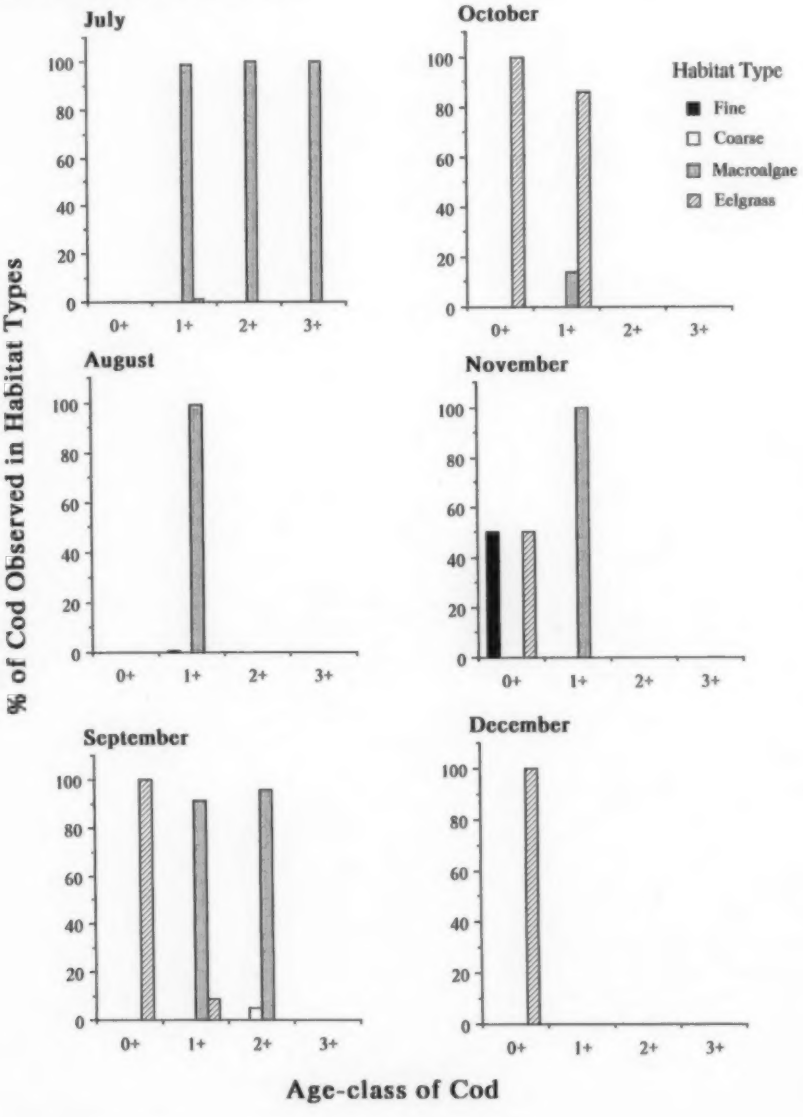
Fig. 2. Percentage of the total number of age 0+, 1+, 2+, or 3+ Atlantic cod observed during a SCUBA survey conducted twice each month from July to December 1993 with respect to the habitat type present at the location where the fish were observed (fine = mud, sand, and (or) gravel; coarse = rocks, boulders, and (or) rocky reef; macroalgae = coarse with attached macroalgae (*Chorda tomentosa* and (or) *Agarum cribrosum*); eelgrass = beds of eelgrass (*Zostera marina*)).



could distinctly be felt by the divers at this site from July to November (mean ± 1 SE temperature above 15 m = 9.6 ± 0.1°C and below 15 m = 6.2 ± 0.2°C, as recorded in September 1993; unfortunately, actual temperatures were not recorded at other times during this study).

In addition to juvenile cod, eight other fish species were also recorded at the four SCUBA sites. Of these eight species, *Pleuronectes americanus*, *Tautogolabrus adspersus*, *Myoxocephalus scorpius*, *Ulvaria subbifurcata*, *Raja radiata*, *Hippoglossoides platessoides*, *Pleuronectes ferrugineus*, and *Macrozoarces americanus*, the first three species were most prevalent both throughout the study and at all four SCUBA sites, although the overall number of individuals of a species observed at any one site or time did vary. Of the species observed, shorthorn sculpin (*Myoxocephalus scorpius*) may represent a potential predator to juvenile cod and, therefore, influence their distribution. However, sculpin were recorded at all but site 4, a site where only one age 1+ cod was ever observed. Overall, there appears to be no relationship between substrate use by juvenile cod and the absence/presence of other fish species.

Beach seine survey

Analysis of the beach seine survey data resulted in a significant

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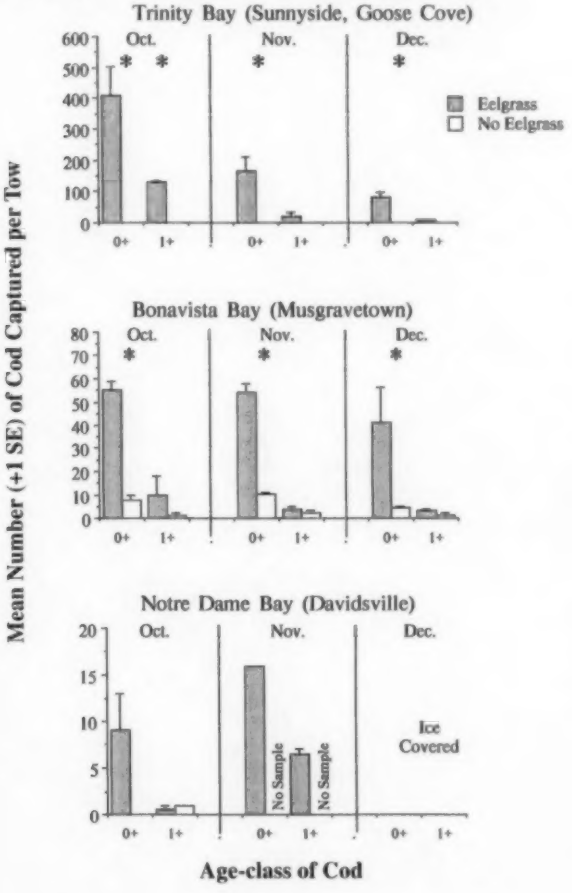
Table 2. Mean (±1 SE) number of juvenile Atlantic cod observed by two divers in association with a rocky substrate with macroalgae at SCUBA survey site 1 (age of juvenile cod indicated by number in parentheses: 0+, 1+, 2+, or 3+).

	Month of sampling					
Depth (m)	July	August	September	October	November	December
0–5	0	0	0	0	0	0
5–10	0	0	0	0	0	0
10–15	9.5±5.5 (1+)	0	0.5±0.5 (1+)	0	0	0
15–20	51.8±11.8 (1+)	34.5±9.5 (1+)	97.8±52.4 (1+)			
	1.0±1.0 (2+)		0.5±0.5 (2+)	0	0	0
20–22.5	37.8±5.5 (1+)	25.0±4.0 (1+)	2.0±1.2 (1+)	1.0±1.0 (1+)	1.0±1.0 (1+)	0
	2.0±0.0 (3+)		10.0±3.0 (2+)			

Fig. 3. Mean number of age 0+ and 1+ Atlantic cod captured from eelgrass and no-eelgrass locations in Trinity, Bonavista, and Notre Dame bays, Newfoundland, during a monthly beach December 1994 (asterisk indicates a significant difference in the mean number of fish captured from eelgrass versus no-eelgrass locations).



four-way interaction ($F_{14,30} = 8.54$, $p = 0.0001$). This result suggests that the number of cod from each age-class collected from eelgrass and no-eelgrass locations differed among collection sites (i.e., bays) and (or) time (i.e., months) of collection (Fig. 3).

The overall mean number of juvenile cod collected in October differed among the three sampling sites (Trinity Bay > Bonavista Bay: $t = 8.39$, $p = 0.0001$; Trinity Bay > Notre Dame Bay: $t = 12.59$, $p = 0.0001$; Bonavista Bay > Notre Dame Bay: $t = 4.21$, $p = 0{,}0002$). Unlike October, there was no difference in the number of juvenile cod collected from the Bonavista and Trinity Bay sites in November ($t = 1.62$, $p = 0.11$) and December ($t = 0.26$, $p = 0.79$). No samples could be collected at the no-eelgrass location in November from the Notre Dame Bay site due to extremely high winds, and no samples could be collected from either location at this site in December due to ice cover.

Catches of juvenile cod from the Bonavista and Notre Dame Bay sites (i.e., eelgrass location only in October and November) differed among sites, but remained similar within each of these sites over the sampling period. In contrast, at the Trinity Bay site, there was a significant reduction in the mean number of juvenile cod captured in November ($t = 6.63$, $p = 0.0001$) and December ($t = 9.33$, $p = 0.0001$) as compared with that captured in October.

Three age-classes of juvenile cod (i.e., ages 0+, 1+, and 2+) were captured in October at the Bonavista Bay site. During November and December at the Bonavista Bay site, and at all times at the Trinity Bay and Notre Dame Bay sites, only age 0+ and 1+ cod were collected. Regardless of sampling site or sampling date, samples were dominated by age 0+ cod (Fig. 3). At all but the Notre Dame Bay site, and on all three sampling dates, significantly more age 0+ cod were captured from the location with eelgrass present (Table 3; Fig. 3). Although not statistically significant, the pattern was similar at the Notre Dame Bay site in October. While a similar pattern was observed for age 1+ cod, the number of fish collected from eelgrass versus no-eelgrass locations was only significantly higher from eelgrass at the Trinity Bay site in October (Table 3).

While age 1+ cod were captured at both eelgrass and no-eelgrass locations at all three sites, no age 0+ cod were captured from no-eelgrass locations, except at the Bonavista Bay site. Qualitative observations at this site indicated the presence of a narrow band (3 to 5 m wide) of macroalgae several metres offshore, a feature absent from the other no-eelgrass locations in both Trinity and Notre Dame bays. The age 0+ cod may have been associated with the macroalgae at this location, as was the case for older conspecifics in our SCUBA survey.

As in the SCUBA survey, in addition to juvenile cod, *Pleuronectes americanus*, *Tautogolabrus adspersus*, *Myoxocephalus scorpius*, *Ulvaria subbifurcata*, *Raja radiata*, *Hippoglossoides platessoides*, *Pleuronectes ferrugineus*, and *Macrozoarces*

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americanus were also collected at both eelgrass and no-eelgrass locations at all three sampling sites. All fish species collected in the beach seine survey, with the exception of *Osmerus mordax*, *Hippoglossoides platessoides*, *Cyclopterus lumpus*, *Urophycis tenuis*, and *Gasterosteus aculeatus*, were also present at the SCUBA sites. The lowest number of other fish species and individuals was collected at the Trinity Bay site. The eelgrass location at this site produced the largest catches of age 0+ cod (Fig. 3). All fish species collected at the Trinity Bay site were also present in samples from the Bonavista and Notre Dame Bay sites. Shorthorn sculpin, a potential predator of juvenile cod, was present at all but the no-eelgrass location at the Trinity Bay site. Except for the Trinity Bay site, fish species collected at the no-eelgrass location were also present in catches from the adjacent eelgrass location, although the number of individuals caught did vary between locations for some species.

Laboratory experiment

Age 0+ cod

Results from the MANOVA revealed a significant interaction between substrate combination and predator exposure on the proportion of time that age 0+ cod spent on different substrates (Hotelling–Lawely Trace, $F_{20,492} = 10.30$, $p < 0.0001$). These results indicate that substrate use by juvenile cod varied with exposure to a predator, and the influence of predation risk on substrate use by age 0+ cod differed among the combinations of substrates tested. Given this significant interaction, these data were further analysed using a second MANOVA model examining the effects of substrate combination and predator exposure within substrate combination on substrate use by age 0+ cod. This second model revealed an effect of substrate combination (Hotelling–Lawely Trace, $F_{10,502} = 13.77$, $p < 0.0001$) on substrate use by age 0+ cod. Furthermore, in at least one combination of substrates, use of substrates by age 0+ cod was influenced by the absence or presence of a predator (Hotelling–Lawely Trace, $F_{24,502} = 15.73$, $p < 0.0001$).

Substrate combinations with cobble

In combinations with cobble, results from the least squares means analysis (Table 4) indicated that there was a significant increase in the use of cobble by age 0+ cod when in the presence of a predator, along with a significant reduction in the time that age 0+ cod spent on sand or gravel (Fig. 4). There was also a significant increase in use of vegetation in the presence of a predator when the density of the patch was ≥720 stems/m^2.

Age 0+ cod did not use substrates according to substrate availability before (Csv520: $\chi^2 = 176.6$, Csv720: $\chi^2 = 1368.3$, Cgv1000: $\chi^2 = 106.5$; df = 2, $p < 0.005$), during (Csv520: $\chi^2 = 267.6$, Csv720: $\chi^2 = 62.1$, Cgv1000: $\chi^2 = 85.7$; df = 2, $p < 0.005$), or after (Csv520: $\chi^2 = 64.8$, Csv720: $\chi^2 = 124.8$, Cgv1000: $\chi^2 = 14.29$; df = 2, $p < 0.005$) exposure to a predator (Fig. 4). In these combinations, age 0+ cod preferred sand or gravel over both cobble and vegetation prior to exposure to a predator (Table 5). In contrast, cobble was the preferred substrate in the presence of a predator in all but combination Cgv1000. In this combination, age 0+ cod preferred cobble and the 1000 stems/m^2 patch of vegetation equally, both of which were preferred over gravel (Fig. 4). With a predator present, age 0+ cod showed no significant preference between sand and the patch of vegetation with 520 stems/m^2, but did prefer the patch of vegetation with 720 stems/m^2 over sand (Table 5). Following exposure to a predator, vegetation was again the least preferred substrate (Fig. 4).

Table 3. Results of least squares means analyses, *t*-value (*p*), comparing the number of age 0+ or 1+ juvenile Atlantic cod captured at the eelgrass (E) versus no-eelgrass (NE) locations during each of the three months of sampling at the three sampling sites.

	Sampling month		
Sampling site	October	November	December
	Age 0+		
Trinity Bay	18.34 (0.0001)* (E > NE)	11.68 (0.0001)* (E > NE)	8.29 (0.0001)* (E > NE)
Bonavista Bay	4.30 (0.0002)* (E > NE)	3.75 (0.0008)* (E > NE)	3.81 (0.0006)* (E > NE)
Notre Dame Bay	2.67 (0.01)	No data	No data
	Age 1+		
Trinity Bay	9.97 (0.0001)* (E > NE)	3.37 (0.002)	2.28 (0.03)
Bonavista Bay	1.94 (0.06)	0.56 (0.58)	1.06 (0.29)
Notre Dame Bay	0.46 (0.65)	No data	No data

Note: *Significant difference in the number of age 0+ or 1+ cod captured in the E versus NE location (test significant if $p < 0.001$; p corrected using the Bonferroni method). E > NE: significantly more fish captured in the E versus NE location.

Substrate combinations with no cobble

In combinations lacking cobble, there was a significant increase in the use of vegetation by age 0+ cod when in the presence of a predator (Table 4). This was true for all three densities of vegetation tested (Fig. 4).

In combinations with sand, gravel, and vegetation, age 0+ cod did not use these three substrates equally before (Sgv520: $\chi^2 = 134.7$, Sgv720: $\chi^2 = 655.2$, Sgv1000: $\chi^2 = 708.2$; df = 2, $p < 0.005$), during (Sgv520: $\chi^2 = 147.9$, Sgv720: $\chi^2 = 62.8$, Sgv1000: $\chi^2 = 277.6$; df = 2, $p < 0.005$), or after (Sgv520: $\chi^2 = 27.4$, Sgv720: $\chi^2 = 15.7$, Sgv1000: $\chi^2 = 130.5$; df = 2, $p < 0.005$) exposure to a predator (Fig. 4). Age 0+ cod showed a preference for gravel over sand both before and after exposure to a predator in all three combinations (Table 5). Prior to exposure to a predator, vegetation was the least preferred substrate in all but combination Sgv520, where it was preferred over sand (Fig. 4). In the presence of a predator, age 0+ cod showed a significant preference for vegetation in all three combinations (Table 5). Following exposure to a predator, gravel was again the preferred substrate in all combinations (Fig. 4).

Predator (age 3+ cod)

In all combinations, predators did not use the substrates as available (Csv520: $\chi^2 = 7.1$, Csv720: $\chi^2 = 34.6$, Cgv1000: $\chi^2 = 13.2$, Sgv520: $\chi^2 = 18.3$, Sgv720: $\chi^2 = 22.1$, Sgv1000: $\chi^2 = 6.14$; df = 2, $p < 0.05$) (Fig. 5). Substrate use by the predators (Table 6) showed no consistent pattern of preference.

When in the presence of a predator, the pattern of substrate use by age 0+ cod may have been the result of (1) predator avoidance and (or) (2) selection of substrates based on the

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Table 4. Results of least squares means analyses, *t*-value (*p*), for effects of predator exposure (BP = before, DP = during, and AP = after exposure to a predator) on time spent on substrates by juvenile Atlantic cod within each combination of substrates tested (see text for definition of combinations).

		Predator exposures compared		
Combination	Substrate	BP vs. AP	BP vs. DP	DP vs. AP
Csv520	Cobble	1.65 (0.10)	5.44 (0.0001)* (DP > BP)	2.24 (0.027)
	Sand	0.93 (0.35)	6.10 (0.0001)* (BP > DP)	3.33 (0.001)* (AP > DP)
	Vegetation	1.03 (0.30)	0.59 (0.55)	0.52 (0.60)
Csv720	Cobble	1.97 (0.05)	6.21 (0.0001)* (DP > BP)	2.48 (0.014)
	Sand	2.34 (0.02)	11.32 (0.0001)* (BP > DP)	5.64 (0.0001)* (AP > DP)
	Vegetation	0.09 (0.92)	3.37 (0.001)* (DP > BP)	2.39 (0.02)
Cgv1000	Cobble	3.47 (0.0001)* (AP > BP)	3.86 (0.0001)* (DP > BP)	0.95 (0.34
	Gravel	1.76 (0.08)	5.73 (0.0001)* (BP > DP)	2.34 (0.02)
	Vegetation	0.51 (0.61)	3.86 (0.0001)* (DP > BP)	3.47 (0.0006)* (DP > AP)
Sgv520	Sand	0.17 (0.86)	4.13 (0.0001)* (DP > BP)	2.97 (0.003)* (DP > AP)
	Gravel	0.67 (0.51)	5.79 (0.0001)* (BP > DP)	4.55 (0.0001)* (AP > DP)
	Vegetation	0.61 (0.55)	2.83 (0.0053)* (DP > BP)	2.47 (0.014)
Sgv720	Sand	0.09 (0.92)	1.67 (0.10)	1.05 (0.29)
	Gravel	2.54 (0.01)	5.30 (0.0001)* (BP > DP)	1.35 (0.18)
	Vegetation	2.97 (0.004)* (AP > BP)	7.51 (0.0053)* (DP > BP)	2.47 (0.02)
Sgv1000	Sand	2.01 (0.05)	4.67 (0.0001)* (BP > DP)	1.39 (0.16)
	Gravel	0.74 (0.46)	5.69 (0.0001)* (BP > DP)	4.56 (0.0001)* (AP > DP)
	Vegetation	0.98 (0.33)	10.48 (0.0001)* (DP > BP)	6.31 (0.0001)* (DP > AP)

Note: *Significant difference in the time juveniles spent on that substrate between predator exposures (test significant if $p < 0.0056$; p corrected using the Bonferroni method). Predator exposure: e.g., DP > BP indicates that for any given substrate, significantly more time was spent on that substrate DP versus BP.

refuge they provide from predation. Results from the multiple contingency tables analysis indicated that for at least one combination of substrates, there was some relationship between substrate use by the age 0+ cod and that of the predator ($\chi^2 = 597.65$, df = 4, $p < 0.005$). Analyses within combinations (Table 7) revealed that a relationship between substrate use by the age 0+ cod and predator existed in all but combination Csv520. In this combination, both age 0+ cod and predators preferred the cobble (Fig. 5), indicating that simple avoidance of the predator by the age 0+ cod would not explain their use of substrates. Similarly, in combination Sgv1000, both the predator and age 0+ cod used the patch of vegetation, again indicating that substrate use by age 0+ cod was not simply predator avoidance (lambda = 0.000, ASE = 0.000). In combination Csv720, age 0+ cod preferred cobble, while the predator preferred sand (Fig. 5). These results could be interpreted as predator avoidance by the age 0+ cod. However, results from the lambda association measures analysis indicated that information on the predator's use of substrate would not increase the accuracy of predicting substrate use by age 0+ cod (lambda = 0.004, ASE = 0.028; lambda/ASE < 2), indicating that use of cobble by the age 0+ cod in this combination was not simply predator avoidance. In contrast, in combinations Sgv720 and Sgv520, lambda association measures indicated that substrate use by age 0+ cod could be more accurately predicted given information on the predator's use of substrates (Sgv520: lambda = 0.160, ASE = 0.039; Sgv720: lambda = 0.183, ASE = 0.048). These results indicate that in these combinations, substrate use by age 0+ cod was the result of the age 0+ fish avoiding the predator's location, and qualitative observations support this conclusion (Fig. 5). Finally, in combination Cgv1000, age 0+ cod used cobble and vegetation equally when exposed to a predator, while the predator used cobble and gravel, but avoided the vegetation (Fig. 5). Use of

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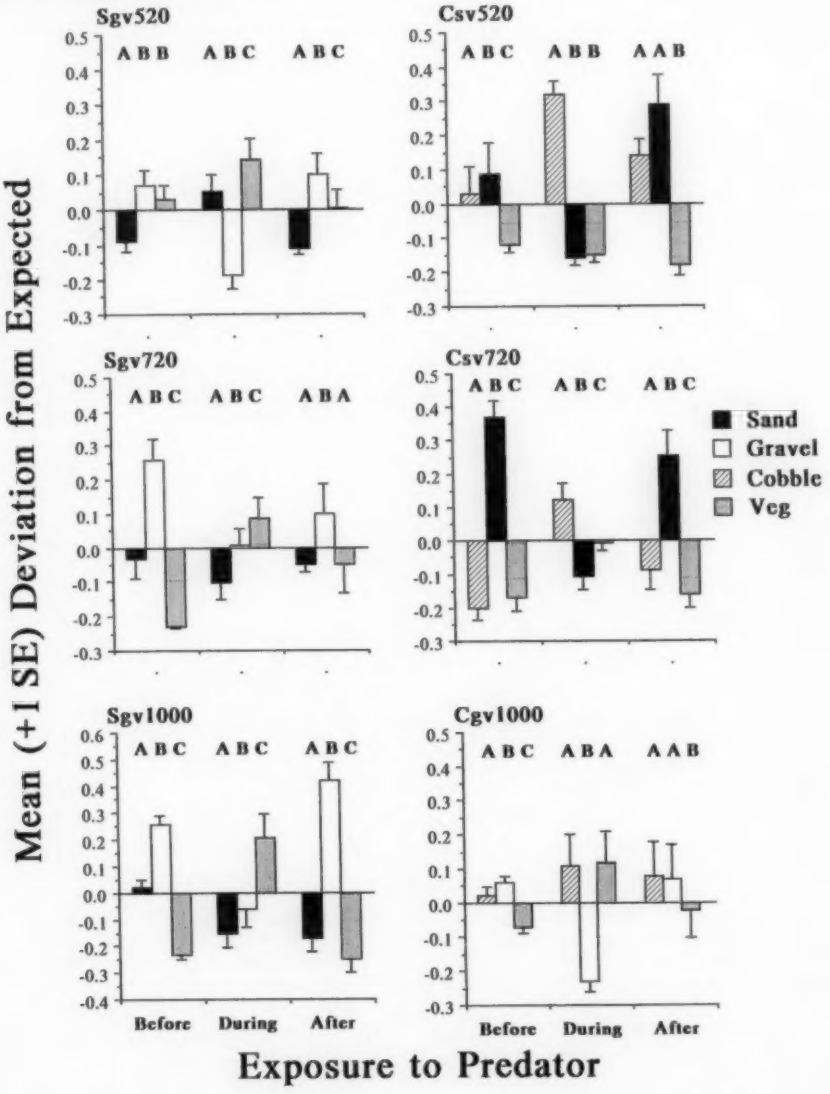
Fig. 4. Mean deviation from the number of juvenile Atlantic cod expected to use each substrate before, during, and after exposure to a predator, assuming that use of substrates is according to their availability (i.e., no preference = 0 on graph) (see text for definition of substrates). Within each predator exposure (i.e., before, during, and after exposure to predator), bars with different letters above them indicate a significant difference in the use of those substrates.



cobble by both the predator and age 0+ cod would suggest that substrate use by age 0+ cod was not simply predator avoidance. However, use of the vegetation by the age 0+ cod may well have been, and results from lambda association measures suggest that predator avoidance did play a role (lambda = 0.061, ASE = 0.023; lambda/ASE > 2).

There was a significant difference in both latency until the first age 0+ cod was captured ($F_{5,32} = 8.41$, $p < 0.0001$) and the number of age 0+ cod captured ($F_{5,32} = 5.99$, $p < 0.0001$) among the different combinations of substrates tested (Fig. 6). It took the predator significantly longer to capture an age 0+ cod in combinations with cobble or the patch of vegetation with 1000 stems/m^2 as compared with those lacking these substrates. Between combinations Sgv720 and Sgv520, it took the predator significantly longer to capture an age 0+ cod when the patch of vegetation with 720 stems/m^2 was present. Significantly fewer age 0+ cod were captured when cobble or the patch of vegetation with 1000 stems/m^2 was present, and there was no significant difference in the mean number of age 0+ cod captured in combinations lacking cobble, regardless of the density of vegetation present (Fig. 6). Taken together, these results suggest that cobble offers the greatest safety from predation to juvenile cod, with vegetation offering safety depending on the density of stems present.

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Table 5. Results of chi-square goodness-of-fit tests examining substrate use by juvenile Atlantic cod within each substrate combination and predator exposure (substrates and predator exposures as in Table 1).

Combination	Substrates	χ^2	Summary of substrate preference
Csv520 BP	Cobble and sand	15.6*	Sand > cobble > v520
	Cobble and v520	122.6*	
	Sand and v520	181.0*	
Csv520 DP	Cobble and sand	173.0*	Cobble > sand = v520
	Cobble and v520	129.1*	
	Sand and v520	0.5	
Csv520 AP	Cobble and sand	0.6	Cobble = sand > v520
	Cobble and v520	70.6*	
	Sand and v520	56.9*	
Csv720 BP	Cobble and sand	791.7*	Sand > cobble > v720
	Cobble and v720	53.3*	
	Sand and v720	758.9*	
Csv720 DP	Cobble and sand	72.2*	Cobble > v720 > sand
	Cobble and v720	16.8*	
	Sand and v720	18.9*	
Csv720 AP	Cobble and sand	44.8*	Sand > cobble > v720
	Cobble and v720	32.5*	
	Sand and v720	106.3*	
Cgv1000 BP	Cobble and gravel	18.1*	Gravel > cobble > v1000
	Cobble and v1000	38.1*	
	Gravel and v1000	107.2*	
Cgv1000 DP	Cobble and gravel	38.5*	Cobble = v1000 > gravel
	Cobble and v1000	1.6	
	Gravel and v1000	80.9*	
Cgv1000 AP	Cobble and gravel	3.9*	Cobble > v1000 = gravel
	Cobble and v1000	14.1*	
	Gravel and v1000	3.2	
Sgv520 BP	Sand and gravel	155.2*	Gravel = v520 > sand
	Sand and v520	117.6*	
	Gravel and v520	1.6	
Sgv520 DP	Sand and gravel	38.3*	v520 > sand > gravel
	Sand and v520	17.0*	
	Gravel and v520	125.4*	
Sgv520 AP	Sand and gravel	33.5*	Gravel > v520 > sand
	Sand and v520	12.1*	
	Gravel and v520	4.7*	
Sgv720 BP	Sand and gravel	135.3*	Gravel > sand > v720
	Sand and v720	293.8*	
	Gravel and v720	522.3*	
Sgv720 DP	Sand and gravel	18.8*	v720 > gravel > sand
	Sand and v720	41.3*	
	Gravel and v720	8.9*	
Sgv720 AP	Sand and gravel	9.5*	Gravel > v720 = sand
	Sand and v720	0.8	
	Gravel and v720	16.0*	
Sgv1000 BP	Sand and gravel	79.3*	Gravel > sand > v1000
	Sand and v1000	351.2*	
	Gravel and v1000	725.8*	
Sgv1000 DP	Sand and gravel	8.2*	v1000 > gravel > sand
	Sand and v1000	214.1*	
	Gravel and v1000	143.5*	
Sgv1000 AP	Sand and gravel	59.8*	Gravel > sand > v1000
	Sand and v1000	8.0*	
	Gravel and v1000	107.5*	

Note: *Significant difference in the use of substrates by the juvenile cod. Results were compared with $\chi^2 = 3.84$, df = 1, $p = 0.05$. Summary of substrate preference: e.g., cobble > sand = v520 indicates a significant preference for cobble over sand and v520 and no significant preference between sand and v520.

When data from this experiment were compared with data from an earlier study (Gotceitas and Brown 1993) investigating the use of sand, gravel, and cobble by age 0+ cod in the absence and presence of a predator, again the latency to first capture ($F_{8,45} = 13.03$, $p < 0.0001$) and number of age 0+ cod caught ($F_{8,45} = 4.38$, $p < 0.0006$) differed significantly among substrate combinations. Predators captured age 0+ cod in the shortest amount of time in combinations lacking both cobble and vegetation. This was followed by combination Sgv520 and then combination Sgv720, and finally it took predators the longest to capture a juvenile cod in those combinations with cobble or the patch of vegetation with 1000 stems/m^2. Results comparing the mean number of age 0+ cod captured indicated that the lowest number captured occurred in combinations with cobble or vegetation at a density of 1000 stems/m^2. This was followed by those with vegetation, and finally the highest number of age 0+ cod were captured in combinations lacking both vegetation and cobble (i.e., sand and gravel).

Discussion

Our field work demonstrates that age 0+ Atlantic cod use eelgrass beds as a nearshore habitat in Newfoundland, Canada. Among the different habitat types, age 0+ cod were found almost exclusively in eelgrass, and this usage was consistent spatially and temporally. Our results are consistent with reports from Norway (Tveite 1984), Denmark (Støttrup et al. 1994), and Nova Scotia, Canada (Tupper and Boutilier 1995*b*), suggesting that juvenile cod use eelgrass as a habitat. In discussing the results from a survey for age 0+ Atlantic cod along the Skagerrak coast of Norway, conducted annually since 1917, Tveite (1984) reported an apparent connection between the decline in numbers of juvenile cod at certain sampling sites and the disappearance of eelgrass from these sites. In Nova Scotian habitat types similar to those sampled in our study, Tupper and Boutilier (1995*b*) reported significantly higher growth rates for age 0+ cod from eelgrass. Overall, the evidence suggests that eelgrass is an important nearshore habitat for age 0+ Atlantic cod, and therefore, protection of this habitat should be an important consideration with respect to the conservation of nearshore nursery habitat and the management of Atlantic cod.

While our study demonstrates that the presence of eelgrass is important in determining the distribution of age 0+ cod in the nearshore environment of Newfoundland, other factors appear also to play a role. For example, numbers of age 0+ cod collected during our beach seine survey were always lowest at the Notre Dame Bay eelgrass site, which was also the shallowest

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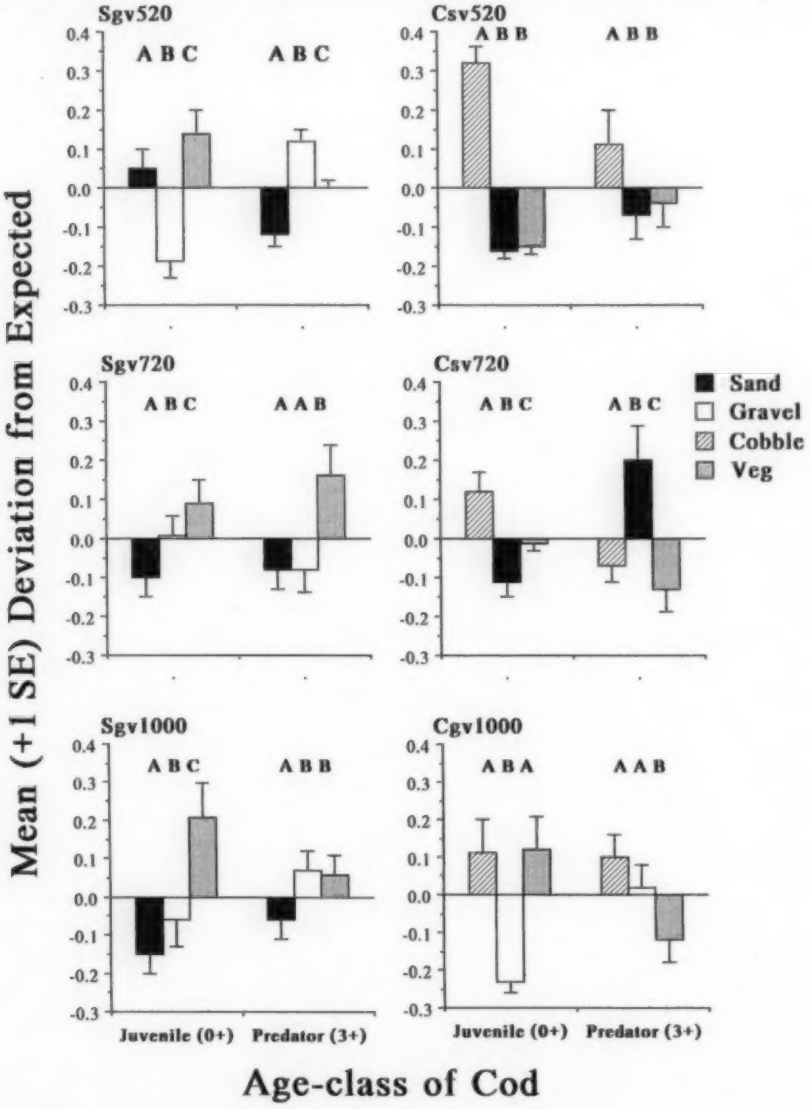
Fig. 5. Comparison of substrate use by juvenile Atlantic cod when in the presence of a predator with that of the predator (see text for definition of substrates). Bars with different letters above them indicate a significant difference in the use of those substrates by the juveniles or predator.



and least saline site sampled (Table 1). This would suggest that overall depth and salinity at a site may be important. The eelgrass location that produced the largest catches of age 0+ cod was in a small cove in Trinity Bay and was, by far, the most sheltered eelgrass location we sampled with respect to physical disturbance. Therefore, the level of exposure at a site may also significantly influence its suitability as a habitat for age 0+ cod. All our field work was conducted during the day. In their study at Bellevue in Trinity Bay, Methven and Bajdik (1994) found age 0+ cod in association with a substrate of small rocks and gravel, but the majority of these fish were collected at night. In contrast, results from some ongoing work on nearshore habitat use by juvenile cod in Newfoundland (V. Gotceitas, personal observations, unpublished data) have revealed no significant difference in the number of age 0+ cod caught from an eelgrass habitat when sampled during the day or night. These results suggest that time-of-day may also influence the use of certain habitats by juvenile cod. In our SCUBA survey, we found age 1+, 2+, and 3+ cod primarily associated with a habitat of rocks and macroalgae; however, the depth and (or) temperature at which this habitat occurred seemed to influence its use by these fish. Finally, while there was no obvious influence due to the absence/presence of other fish species on juvenile cod distribution in our study, interspecific interactions might, nevertheless, be important under certain conditions. Together, these various results and observations indicate that

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Table 6. Results of chi-square goodness-of-fit tests examining substrate use by the predators (age 3+ Atlantic cod) within each substrate combination (substrates as in Table 1).

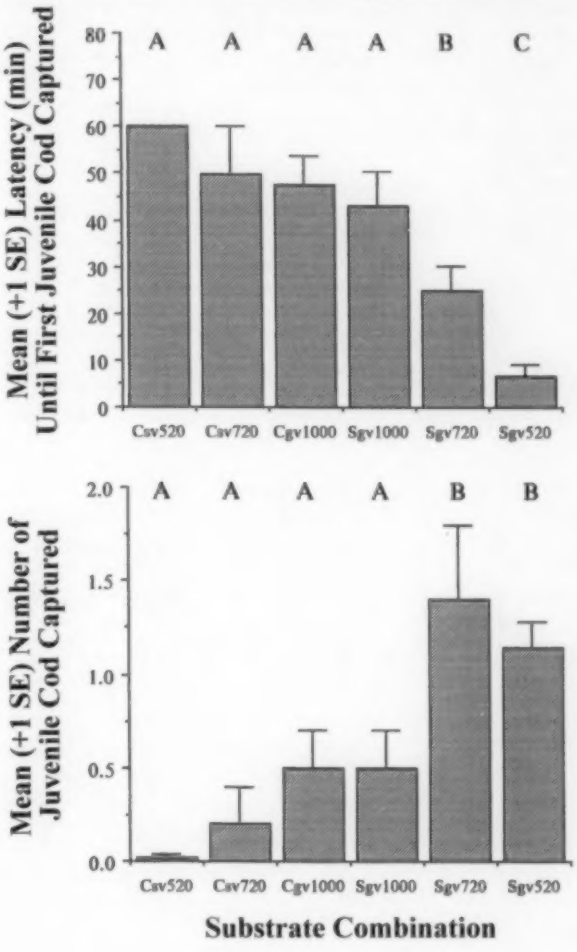
Combination	Substrates	χ^2	Summary of substrate preference
Csv520	Cobble and sand	7.6*	Cobble > sand = v520
	Cobble and v520	4.4*	
	Sand and v520	0.4	
Csv720	Cobble and sand	14.4*	Sand > cobble > v720
	Cobble and v720	6.5*	
	Sand and v720	28.2*	
Cgv1000	Cobble and gravel	0.007	Cobble = gravel > v1000
	Cobble and v1000	11.2*	
	Gravel and v1000	10.7*	
Sgv520	Sand and gravel	21.9*	Gravel > v520 > sand
	Sand and v520	8.5*	
	Gravel and v520	4.2*	
Sgv720	Sand and gravel	1.7	v720 > sand = gravel
	Sand and v720	15.7*	
	Gravel and v720	11.7*	
Sgv1000	Sand and gravel	6.2*	Gravel > sand = v1000
	Sand and v1000	1.9	
	Gravel and v1000	1.2	

Note: *Significant difference in the use of substrates by the predators. Results were compared with $\chi^2 = 3.84$, df = 1, $p = 0.05$. Summary of substrate preference: e.g., cobble > sand = v520 indicates a significant preference for cobble over sand and v520 and no significant preference between sand and v520.

Table 7. Results of the multiple contingency tables analyses investigating whether substrate use by juvenile Atlantic cod was independent of that by the predator in the different combinations of substrates tested (substrates as in Table 1).

Combination	χ^2	df	p	n
Csv520	6.91	4	0.141	694
Csv720	265.38	4	0.0001	1467
Cgv1000	36.89	4	0.0001	832
Sgv520	125.56	4	0.0001	852
Sgv720	118.50	4	0.0001	637
Sgv1000	131.94	4	0.0001	1398

Fig. 6. Mean latency until the predator captured a juvenile Atlantic cod and mean number of juvenile cod captured by the predator during the 60 min that the predator had access to the juveniles. Bars with different letters above them indicate a significant difference.



more information is needed on the various abiotic and biotic factors affecting habitat use by juvenile cod, if we are to better understand factors influencing their distribution.

Tupper and Boutilier (1995*b*) found higher densities of age 0+ cod in cobble and rock reef habitats than in eelgrass. They attributed their results to variation in postsettlement survival among habitat types due to increased shelter and decreased risk of predation to age 0+ cod in the cobble and rock reef habitats. In a series of laboratory studies, Gotceitas and Brown (1993) and Gotceitas et al. (1995) demonstrated that age 0+ cod significantly reduced their risk to predation by seeking shelter in the interstitial spaces of a cobble substrate or in a patch of artificial macroalgae. Based on the above results, and their demonstrated eelgrass preference, we would have expected to find age 0+ cod also using habitats with coarse mineral substrates and macroalgae. However, no age 0+ cod were found in such habitat. Segregation with respect to habitat use by different age- or size-classes within a population has been noted in a variety of organisms (e.g., Kneib 1987; Sweitzer and Berger 1992; Wissinger 1992). For example, in Newfoundland, juvenile Atlantic cod appear to be concentrated in nearshore and inshore habitats, while adults inhabit inshore and offshore areas (Lilly 1987). Being cannibalistic (Bogstad et al. 1994), habitat segregation between juvenile and adult cod may, in part at least, represent direct and indirect (e.g., predator avoidance) effects of predation on the juvenile fish. In our study, while some overlap did occur, age 0+ cod were primarily found in eelgrass, while age 1+ cod appeared to be concentrated in areas of coarse bottom with macroalgae. If, as suggested by Tupper and Boutilier (1995*b*), the distribution of age 0+ cod is determined by variation in postsettlement survival among habitat types, the absence of age 0+ cod from the coarse bottom with macroalgae habitat observed in our study may be due to cannibalism by the age 1+ cod (Fraser et al. 1996). In addition to such direct effects of predation, the distribution of age 0+ cod among habitats might

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also be the result of indirect effects of predators, such as predator avoidance. In their study with age 0+ and 1+ cod, Fraser et al. (1996) demonstrated that when tested alone, both age 0+ and 1+ cod preferred the same bottom substrate types, but when in the presence of age 1+ conspecifics, age 0+ fish altered their use of substrates to avoid the age 1+ fish. Unlike our study, there was no mention of older age-classes of cod inhabiting the study site examined by Tupper and Boutilier (1995*b*). This being the case, one possible explanation for the difference in habitat use by age 0+ cod observed between our study and that of Tupper and Boutilier (1995*b*) may be the presence and absence of older conspecifics.

Use of eelgrass by age 0+ cod may, in part at least, be related to shelter from predation. A variety of organisms use seagrass beds as a refuge from predation (Orth et al. 1984), and our laboratory experiment indicated that patches of artificial vegetation resembling eelgrass can provide age 0+ cod with protection from predators. For example, we found that the presence of eelgrass significantly increased the time required by a predator to capture an age 0+ cod and decreased the number of age 0+ cod captured. In our study, protection from predation to age 0+ cod increased as the density of plant stems in the patch of vegetation increased. A similar positive relationship between the refuge potential of aquatic vegetation and increasing plant stem density has been noted in a number of other studies in both marine and freshwater systems (e.g., Orth et al. 1984; Gotceitas and Colgan 1989). More specifically, it has been suggested that this relationship resembles a "step-function" (Nelson 1979) whereby some threshold level of habitat complexity (e.g., plant stem density) is necessary before a patch of vegetation offers a refuge from predation (Gotceitas and Colgan 1989; Isaksson et al. 1994; but see Nelson and Bonsdorff 1990). In the present study, a density of 1000 stems/m^2 both significantly increased the time required by a predator to capture a juvenile cod and reduced the number of juveniles captured. In comparison, while it took the predator significantly longer to capture a juvenile cod in the presence of 720 versus 520 stems/m^2, there was no significant difference in the number of age 0+ cod captured between these two densities of vegetation. These results suggest that, in our study, a threshold level of habitat complexity above which our patches of eelgrass provided a significant reduction in predation risk to age 0+ cod may exist between 720 and 1000 stems/m^2. Overall, our results suggest that age 0+ cod could find refuge from predation in eelgrass beds, but that the level of protection offered would vary with variation in plant stem density. The actual density of plants required may differ from that suggested by our laboratory experiment, depending on how accurately our artificial eelgrass mimics natural conditions (i.e., artificial seagrass units attract fish assemblages typical of real seagrass beds; Bell et al. 1985; Sogard 1989).

Safety from predators may not be the only reason age 0+ cod use eelgrass beds. Eelgrass is known to provide a habitat for a wide variety of invertebrates (e.g., Orth et al. 1984), and Tupper and Boutilier (1995*b*) found growth rate of age 0+ cod to be highest in an eelgrass habitat. Therefore, while a coarse mineral substrate may offer age 0+ cod the greatest protection from predators (Gotceitas and Brown 1993; Gotceitas et al. 1995; Tupper and Boutilier 1995*b*), given that our results show that eelgrass can also provide age 0+ cod with refuge from predation, use of eelgrass by age 0+ cod may represent selection for a habitat offering both rapid growth and safety. Selection among habitats on the basis of a compromise between safety and foraging has been demonstrated in other organisms (e.g., Gilliam and Fraser 1987; Gotceitas and Colgan 1989).

In summary, our results demonstrate that age 0+ Atlantic cod use eelgrass beds as a habitat that may offer saftey from predation in the nearshore environment of Newfoundland; such use may be influenced by a variety of abiotic factors and avoidance of older conspecifics. Our laboratory results suggest that the safety offered by eelgrass varies with plant stem density. If eelgrass beds represent an "essential habitat" (sensu Langton et al. 1996) for age 0+ cod in the nearshore environment of Newfoundland, and elsewhere, natural or anthropogenically induced fluctuations in the availability of this habitat may limit recruitment of cod. Such limitation on recruitment has been documented for fish in relation to macroalgal dynamics (Anderson 1994; Carr 1994). To determine whether this is the case for juvenile cod, work is needed to determine the influence that variation in eelgrass habitat (e.g., patch size, patch distribution, etc.) might have on juvenile cod distribution and survival.

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Transfer of mercury from benthic invertebrates to fishes in lakes with contrasting fish community structures

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Abstract: We examined the flow of mercury (Hg) from benthic invertebrates to fishes in lakes with contrasting fish community structure. The study was carried out in two whole lakes in southcentral Ontario in 1992. Both were remote from direct sources of contamination and were chosen because of their physical and chemical similarities. Although the fish communities in the two lakes were qualitatively similar, the total number of fishes in Ranger Lake was an order of magnitude smaller than that in Mouse Lake. As a result of the lower net predation from benthivorous fishes, documented in earlier studies, Ranger Lake benthic invertebrate populations were significantly higher. However, benthic invertebrate taxa in Mouse Lake were generally larger and had higher Hg concentrations. This was partly attributed to the stunted growth of Mouse Lake fishes, which did not allow them to prey on larger benthos as a result of gape limitations. Despite the lower Hg concentrations in Ranger Lake benthos, total benthic invertebrate Hg pools were higher in this lake as a result of its higher total benthic invertebrate biomass. However, the transfer of total Hg from benthic invertebrates to fishes was higher in Mouse Lake due to the higher consumption rates of benthivorous fishes.

Résumé : Nous avons examiné le flux du mercure (Hg) des invertébrés benthiques aux poissons dans des lacs ayant des communautés de poissons de structure différente. L'étude a été réalisée dans deux lacs entiers dans le centre-sud de l'Ontario en 1992. Les deux lacs étaient éloignés des sources de contamination directe et ils ont été choisis en raison de leur ressemblance du point de vue physique et chimique. Bien que les communautés de poissons dans les deux lacs aient été semblables du point de vue qualitatif, le nombre total de poissons dans le lac Ranger était inférieur d'un ordre de grandeur à celui du lac Mouse. À cause de la prédation nette inférieure attribuable aux poissons benthivores, documentée dans des études antérieures, les populations d'invertébrés benthiques du lac Ranger étaient substantiellement plus importantes. Cependant, les représentants des taxons d'invertébrés benthiques du lac Mouse étaient généralement de taille plus grande et avaient des concentrations de Hg plus élevées. Cette situation était en partie attribuable à la croissance arrêtée des poissons du lac Mouse, qui ne leur permettait pas de consommer les organismes benthiques plus gros en raison d'une ouverture maximale de la bouche insuffisante. Malgré les concentrations de Hg inférieures dans le benthos du lac Ranger, les pools de Hg chez les invertébrés benthiques étaient plus importants dans ce lac en raison de sa biomasse totale en invertébrés benthiques plus élevée. Toutefois, le transfert de Hg des invertébrés benthiques aux poissons était plus élevé dans le lac Mouse en raison du taux de consommation plus élevé des poissons benthivores.
[Traduit par la Rédaction]

Introduction

Many lakes in North America that have never received direct discharges of mercury-containing contaminants exhibit elevated levels of this metal (Evans 1986; Fitzgerald and Clarkson 1991). This has led to restrictions on the consumption of many species of fish (OMOE and OMNR 1991). Hg concentrations in biota can vary dramatically among uncontaminated lakes, and thus, many studies have attempted to determine possible environmental causes for these differences. With respect to fishes, it is generally believed that Hg bioaccumulation is enhanced by increased acidity (Wren and MacCrimmon 1983; Suns et al. 1987), increased dissolved organic matter (Suns et al. 1987; Mierle and Ingram 1991), decreased water hardness (Rodgers and Beamish 1983), and decreased alkalinity (Wiener and Stokes 1990; Spry and Wiener 1991).

Except for a few studies, ecological considerations generally have been ignored as possible factors that may influence contaminant bioaccumulation. Field studies have shown that Hg accumulation in fishes is highly influenced by diet (MacCrimmon et al. 1983; Mathers and Johansen 1985). Rasmussen et al. (1990) and Futter (1994) have found that food web structure can influence PCB and Hg concentrations, respectively, in top fish predators. In addition, when total fish populations have changed, fishes that occupy a lower trophic level also show changes in Hg accumulation as a result of shifts in diets and growth rates (Verta 1990). It is not known whether there is any between-lake variability in Hg accumulation among littoral zone biota resulting from differences in trophic structures. While there is no empirical evidence available, such differences are predicted to be significant (Rasmussen et al. 1990).

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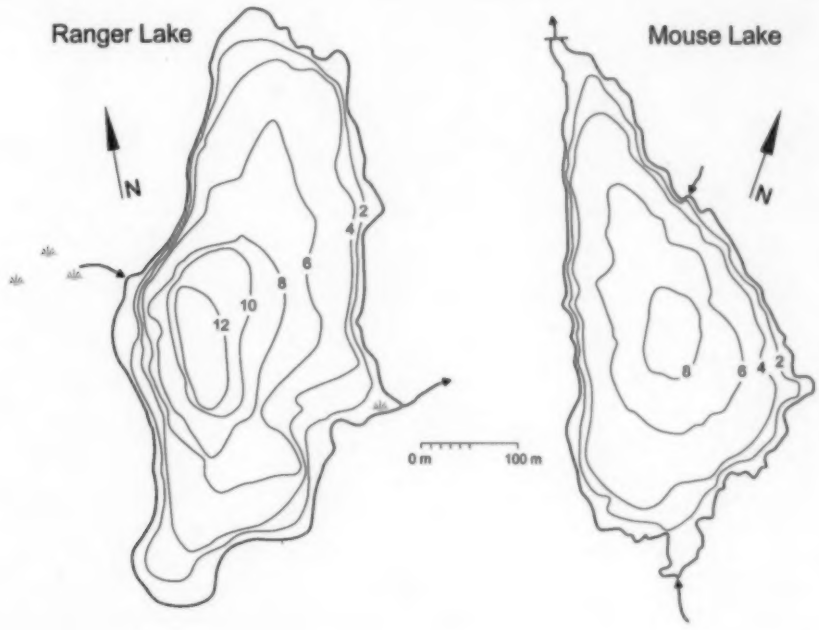
Fig. 1. Bathymetric maps of Ranger and Mouse lakes. Depth intervals are indicated in metres. Arrows adjacent to lakes indicate inflows and outflows.



The purpose of this study was to determine whether contrasting fish community structures would affect benthic invertebrate Hg concentrations, benthic invertebrate Hg pools, and the flow of Hg from benthos to fishes. Since invertebrate size is correlated with Hg concentrations, Hg accumulation in benthic invertebrates may be affected as a result of decreased size caused by predatory stress (Feltmate and Williams 1991; Parkman and Meili 1993). Conversely, Hg bioaccumulation in fish predators also can be affected because of differences in available diet (MacCrimmon et al. 1983). Although the pool of Hg found in benthic invertebrates may not necessarily reflect the amount of Hg consumed by benthivorous fishes, it can be helpful as a measure of the cycling of Hg. Mouse Lake and Ranger Lake were chosen for this study because of their contrasting fish trophic structures, although the species of fishes present in the two lakes were similar (Rocchi 1993; Popiel 1994; Ramcharan et al. 1995). Furthermore, the physical and chemical similarities between the two lakes diminish the possibilities of differences in Hg accumulation by influences other than fish community structure (Ramcharan et al. 1995).

Study site description

Mouse Lake (45°11′N, 78°5′W) and Ranger Lake (45°09′N, 78°51′W) are located in the Muskoka region of southcentral Ontario (Fig. 1). Mouse and Ranger lakes have surface areas of 9.0 and 11.2 ha and maximum depths of 9.0 and 13.0 m, respectively. In addition, their water chemistries are very similar (Table 1) (Ramcharan et al. 1995). *Brasenia* sp., *Pontederia* sp., and *Potamogeton* sp. are the dominant macrophytes present in the two lakes.

The total Hg concentrations in the water column in Mouse and Ranger lakes were 1.52 ($n = 6$) and 2.19 ng/L ($n = 7$), respectively (Table 1). In the shallow zone (<1.0 m) the total Hg concentrations in sediments in Mouse and Ranger lakes were 28.1 ($n = 12$) and 29.3 ng/g dry weight (dw) ($n = 12$), respectively. In the 1.0–4.9 m depth zone, total Hg concentrations in sediments were 84.9 ($n = 3$) and 70.8 ng/g dw ($n = 3$) in Mouse and Ranger lakes, respectively. In the deepest zone (5.0–9.0 m), total Hg concentrations in sediments in Mouse Lake (281.8 ng/g dw, $n = 3$) and Ranger Lake (310.8 ng/g dw, $n = 3$) were also similar.

The major fish species present in Mouse and Ranger lakes were alike (Table 2). They included pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), and white sucker (*Catostomus commersoni*). However, the presence of piscivores (smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*M. salmoides*)) in Ranger Lake led to a total fish population (282 fish/ha) that was an order of magnitude smaller than that in Mouse Lake (2152 fish/ha) (Ramcharan et al. 1995). Although the benthivorous fish (yellow perch and pumpkinseed) diets in the two lakes were qualitatively similar (Rocchi 1993; Popiel 1994), the net predation of the benthos was much higher in Mouse Lake because of the higher fish population (Wong 1995). The rate of consumption of benthic invertebrates during the study period by all fishes in Mouse Lake was between 1.5 (July) and 2.7 (August) times greater than in Ranger Lake (Wong 1995). As a result, the total benthic biomass in Ranger Lake was consistently higher than in Mouse Lake at depths <1.0 m.

Methods

Benthic survey

Benthic invertebrates were collected during June, July, and August

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Table 1. Physical and chemical characteristics of Mouse and Ranger lakes, 1992 (1993 and 1994 for sediment and water Hg data, respectively).

Physical/chemical parameter	Mouse	Ranger
Catchment area (ha)	185	260
Surface area (ha)	8.99	11.25
Volume ($m^3 \times 10^5$)	4.39	6.32
Flushing rate ($year^{-1}$)	2.41	2.32
Maximum depth (m)	9.0	13.0
Mean depth (m)	4.88	5.62
Shoreline length (km)	1.59	1.63
Shoreline development	1.50	1.37
pH (epilimnion)	5.62 (0.052)	6.01 (0.068)
pH (metalimnion)	5.44 (0.055)	5.64 (0.035)
pH (hypolimnion)	5.59 (0.055)	5.83 (0.050)
DIC (mg/L)	0.68 (0.215)	0.54 (0.083)
DOC (mg/L)	4.67 (0.198)	4.91 (0.224)
Total alkalinity (mequiv./L)	0.28 (0.0965)	0.62 (0.0431)
Total iron (μg/L)	0.0022 (0.00044)	0.0017 (0.00044)
Total nitrogen (μg/L)	295.0 (11.9)	284.0 (9.9)
Total phosphorus (μg/L)	7.80 (0.58)	5.91 (0.34)
Ca^{2+} (mequiv./L)	0.029 (0.00019)	0.031 (0.00033)
Mg^{2+} (mequiv./L)	0.0252 (0.00019)	0.0289 (0.00028)
Total Hg, water (ng/L)	1.52 (0.06)	2.19 (0.10)
Total Hg, sediment (<1 m) (ng/g dw)	28.10 (9.23)	29.31 (16.40)
Total Hg, sediment (1–4.9 m) (ng/g dw)	84.90 (23.41)	70.83 (57.14)
Total Hg, sediment (5–9 m) (ng/g dw)	281.82 (16.06)	310.89 (6.44)

Note: Chemical values (with the exception of sediment Hg data) are seasonal epilimnetic means. Standard errors are given in parentheses. Adapted from Ramcharan et al. (1995) and D.J. McQueen et al., unpublished data.

Table 2. Fish abundance and biomass (±95% confidence interval) in Mouse and Ranger lakes, 1992.

	Abundance (no./ha)		Biomass (kg/ha)	
Fish species	Mouse	Ranger	Mouse	Ranger
Largemouth bass (*Micropterus salmoides*)	0	48.3 (18.7–125.6)	0	4.4 (1.7–11.4)
Smallmouth bass (*Micropterus dolomieu*)	0	12.7 (4.9–33.0)	0	
Yellow perch (*Perca flavescens*)	594.4 (459.8–768.4)	2.3 (1.2–4.6)	7.1 (5.5–9.1)	0.2 (0.1–0.5)
Pumpkinseed (*Lepomis gibbosus*)	1233.0 (890.6–1707.3)	161.4 (113.5–228.5)	10.8 (7.8–14.9)	4.7 (3.3–6.6)
White sucker (*Catostomus commersoni*)	31.7 (21.9–458)	57.4 (52.7–62.4)	16.2 (11.2–23.4)	18.7 (17.2–20.3)
Golden shiner (*Notemigonus crysoleucas*)	171.3 (132.6–221.5)	—	0.7 (0.5–0.9)	—
Brown bullhead (*Ictalurus nebulosus*)	70.7 (19.3–269.1)	—	2.6 (0.7–9.9)	—
Creek chub (*Semotilus atromaculatus*)	50.1 (74.5–174.4)	—	0.6 (0.4–0.9)	—

Note: Dashes indicate species of fishes that were present but either not tagged or not recaptured. Adapted from Ramcharan et al. (1995).

1992 from Mouse and Ranger lakes. Approximately 60 benthic samples were collected from each lake during each of these months. Because of the higher benthic populations and benthivorous fish activity recorded in the shallow depth zone (defined as <1.0 m) (Post and Cucin 1984; N.C. Collins, Erindale Campus, University of Toronto, Toronto, Ont., personal communication), greater sampling effort (60%) was devoted to this depth interval. The proportion of lake area occupied by each depth zone >1.0 m was then used to stratify the remaining sampling effort. These depth intervals were 1.0–4.9 and 5.0–9.0 m. Sampling sites within each depth zone were chosen at random.

A metal corer with an internal area of 91 cm^2 (sample depth ~10 cm) was used to obtain shallow samples (<1.0 m). Deeper samples (i.e., >1.0 m) were obtained with an Ekman dredge that had a surface area of 225 cm^2 (sample depth ~20 cm). Two sieves of 53- and 200-μm mesh were used to filter the shallow and deep samples, respectively, because the sediment particle size and volume differed at the various depths. Samples were preserved in 10% formalin solution and stained with rose bengal in the field. The samples were processed by centrifugally floating with saturated $CaCl_2$ to remove sand and cobble (Cromar and Williams 1991). The organisms were then sorted under a dissecting microscope (at 10× magnification) and stored in 70% ethanol. Identification was done using the taxonomic keys in Merritt and Cummins (1978).

A Metler microbalance was used to weigh organisms to the nearest 1 μg immediately after blotting them to remove excess fluid. Weights of individual taxa were obtained by pooling the weights of specimens of each taxon from a single sample. A subset of samples was also dry weighed. Dry weights for all other samples were obtained by multiplying wet weights with taxon-specific conversion factors that varied from 0.09 to 0.22 (Wong 1995). These taxon-specific conversion factors were averages of the ratio of dry weight to wet weight. All benthic masses presented represent dry weights, unless otherwise stated. Mean individual weights were obtained by dividing the pooled taxon weight by the total number of individuals in that sample.

Hg determination

A separate set of benthic invertebrates was collected from Mouse and

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Ranger lakes for Hg analysis. Samples were collected from all depths (i.e., <1.0, 1.0–4.9, and 5.0–9.0 m). Collections were made with a dip net in the shallow zone and a stainless steel Ekman dredge in the deeper zones and then filtered through 200-µm Nitex sieves. Organisms were sorted alive (according to taxon) with clean plastic forceps and trays and then set in a refrigerator for 48 h to purge their stomachs of their contents (Jackson 1988). The organisms were subsequently placed in scintillation vials that were covered with parafilm and placed in Zip-Loc polyethylene bags and frozen for later analysis.

Total Hg was measured through cold vapour atomic absorption spectrophotometry with a Pharmacia mercury monitor, model 100M (Allard and Stokes 1989). Benthic samples were dried at 60°C for 48 h and then weighed (minimum weight ≈5 mg dw). Samples were digested in 2.0 mL of a 1:4 HNO_3 (BDH AnalaR) – H_2SO_4 (Seastar) mixture at 250°C for 6 h and then diluted with ultrapure water upon cooling to room temperature. The following day, 1.5 mL of hydroxylamine hydrochloride (10%) was added to each sample. One hundred and fifty millilitres of 15% stannous chloride (in 10% HCl) was used as the reductant in the final Hg analysis.

Quality assurance/quality control

To avoid contamination of samples, plastic forceps, plastic sorting trays, scintillation vials, and glassware were all thoroughly cleaned with soap and ultrapure water. This was followed by bathing sequentially in 1 M NaOH and 10% HNO_3 for 24 h each. All standards, reagents, dilutions, and glassware were prepared with deionized and double-distilled water.

Total Hg analyses for individual samples were repeated three times or until the peaks varied by no more than 5%. Triplicates of blanks, spiked samples, standard solutions (0.0, 0.1, 0.5, and 1.0 ng Hg/L), and Canadian National Research Council dogfish muscle (Dorm-1) (certified 0.798 mg Hg/kg) were analyzed at the beginning of each batch of samples. Standard solutions of 1.0 ng Hg/mL were analyzed throughout each batch (i.e., every third sample) to ensure accuracy and precision throughout analysis of each batch of samples. The mean (±SE) recovery of Dorm-1 from 27 batches of samples was 99.8% (±2.22), with a range of 75–110%. The reported 95% confidence limits for the Dorm-1 were ±9%. The two batches of National Institute of Standards and Technology sediment standards (No. 8406, reported value of 0.06 µg/g) had a recovery level (±SE) of 85.0% (±1.6). No reported confidence limits were provided for the sediment standards. The recovery (±SE) of spiked samples from 27 batches averaged 95.5% (±2.1), with a range of 73.9–112.4%. Further details of the laboratory setup and conditions are described in Mierle (1990).

Statistical analyses

One-way repeated measures analysis of variance (RMANOVA) and standard one-way ANOVA were used to test for differences between mean benthic biomass (grams per square metre) and Hg concentrations (nanograms per gram) between Mouse and Ranger lakes, respectively. Log(x + 1) transformations were performed on the data to achieve homogeneity of variances and normality. Data are presented in an untransformed state, unless otherwise stated. Hg pools (nanograms per square metre) were estimated by multiplying Hg concentration (nanograms per gram) by the mean biomass (grams per square metre) for each taxon. Note that dry weights and dry Hg concentrations were used for statistical purposes. All statistical analyses were done using the Statistical Analysis System (SAS Institute, Inc. 1982).

Hg consumption analyses

Fish populations were estimated by mark and recapture during May–September 1992 by trap-netting, beach-seining, electrofishing, and hook and line (Ramcharan et al. 1995). Cohort estimates were determined for each species by recording physical parameters (length, weight, and scales) of fishes. Detailed analyses of fish diets were obtained by purging stomach contents. All benthos were identified using keys in Merritt and Cummins (1978) and wet weighed. Fish consumption rates, based on calculations from measured growth, were estimated using the Hewett and Johnson (1992) fish bioenergetics model. Total Hg consumption rates for each species were calculated by multiplying the consumption rates for each benthic invertebrate taxon by their corresponding Hg concentration.

Results

The total estimated benthic invertebrate biomass in the shallow zone (i.e., <1.0 m) was significantly higher in Ranger Lake (one-way RMANOVA, $F = 4.5$, $p = 0.04$) compared with Mouse Lake (Table 3). This corresponded to total benthic biomasses in Ranger Lake that were up to 1.5 times (June) higher than in Mouse Lake. A large proportion of the total benthic biomass from each lake consisted of the Odonata, Chironomidae (larvae), Gastropoda, and Ephemeroptera (in descending order of importance).

In the 1.0–4.9 m depth zone, total benthic biomasses between the two lakes were not statistically different during the three months of the study (one-way RMANOVA, $F = 0.28$, $p = 0.60$) (Table 3). In the 5.0–9.0 m depth zone, the total benthic biomasses were significantly higher in Ranger Lake (one-way RMANOVA, $F = 27.3$, $p = 0.0001$) (Table 3). This resulted in benthic biomasses in Ranger Lake that were 2.4 and 4.3 times higher than in Mouse Lake in July and August, respectively. A large proportion (usually >95%) of the benthic biomass in the 5.0–9.0 m samples comprised chironomid (primarily *Chironomus* spp.) and chaoborid (*Chaoborus* spp.) larvae.

Mean individual weights of benthos were significantly different between the two lakes (one-way RMANOVA, $p < 0.05$) (Table 4). All significant tests indicated that Mouse Lake had larger individuals. This included the Gastropoda ($F = 28.8$, $p = 0.0001$), Chironomidae larvae ($F = 25.1$, $p = 0.0001$), and Ephemeroptera ($F = 19.6$, $p = 0.0003$).

A total of 704 benthic invertebrate samples were measured for total Hg in the two lakes (Table 5). Each sample consisted of several individual specimens of the same taxon combined, except for the Odonata and Gastropoda (and the larger Ephemeroptera and Trichoptera), which were analyzed as individual specimens. In both Mouse and Ranger lakes the lowest Hg concentrations were found in the chaoborid and trichopteran larvae where total Hg concentrations were <100 ng/g dw for both taxa. The highest total Hg concentration was found in the gastropod *Campeloma decisum* in both Mouse Lake (938 ng/g dw) and Ranger Lake (609 ng/g dw). The Mouse Lake Gastropoda (one-way ANOVA, $p = 0.02$), shallow (<1.0 m) Chironomidae ($p = 0.001$), and Odonata ($p = 0.0002$) all had significantly higher Hg concentrations than their Ranger Lake equivalents.

Despite the generally higher concentrations of Hg in benthic invertebrates from Mouse Lake, the benthic invertebrate Hg pools in Ranger Lake were significantly higher (one-way RMANOVA, $F = 10.3$, $p = 0.0002$) at depths of <1.0 m (Fig. 2). The amounts by which they were higher in Ranger Lake than in Mouse Lake were 0.5 (August) to 2.7 (July). In the 5.0–9.0 m depth zone, the benthic Hg pool in Ranger Lake was up to 3.9 times higher (August) than in Mouse Lake. The chironomid larvae consistently had the highest geometric mean Hg pools at all depths in both lakes. They ranged from

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Table 3. Mean benthic biomasses (g/m^2 dw) and standard errors (in parentheses) for benthic invertebrates in all depth zones (<1.0, 1–4.9, and 5–9 m) of Mouse and Ranger lakes, 1992.

Taxon	June		July		August	
	Mouse	Ranger	Mouse	Ranger	Mouse	Ranger
			<1.0 m			
n	25	25	25	25	25	25
Gastropoda	0.191 (0.188)	0.355 (0.158)	0.138 (0.133)	0.101 (0.023)	0.273 (0.208)	0.075 (0.026)
Bivalvia	0.013 (0.006)	0.034 (0.014)	0.013 (0.008)	0.014 (0.005)	0.016 (0.005)	0.017 (0.007)
Amphipoda	0.030 (0.009)	0.129 (0.032)	0.020 (0.006)	0.035 (0.008)	0.038 (0.011)	0.053 (0.011)
Chironomidae-larvae	0.134 (0.021)	0.266 (0.046)	0.067 (0.011)	0.126 (0.017)	0.054 (0.010)	0.094 (0.016)
Chironomidae-pupae	0.004 (0.002)	0.009 (0.002)	0.001 (0.000)	0.003 (0.001)	0.001 (0.000)	0.001 (0.001)
Trichoptera	0.004 (0.002)	0.173 (0.048)	0.008 (0.004)	0.007 (0.005)	0.186 (0.129)	0.152 (0.101)
Ephemeroptera	0.317 (0.156)	0.017 (0.016)	0.155 (0.104)	0.049 (0.037)	0.064 (0.063)	0.204 (0.174)
Odonata	0.411 (0.294)	0.474 (0.170)	0.085 (0.054)	0.248 (0.093)	0.453 (0.184)	0.310 (0.113)
Ceratopogonidae	0.006 (0.002)	0.015 (0.004)	0.003 (0.001)	0.007 (0.002)	0.002 (0.001)	0.004 (0.001)
Acari	0.003 (0.002)	0.002 (0.001)	0.001 (0.001)	0.001 (0.001)	0.001 (0.001)	0.003 (0.001)
Hirudinea	0	0.004 (0.002)	0.001 (0.001)	0.006 (0.003)	0	0
Coleoptera	0.025 (0.006)	0.133 (0.093)	0.009 (0.003)	0.033 (0.011)	0.008 (0.003)	0.026 (0.005)
Oligochaeta	0.019 (0.010)	0.069 (0.045)	0.013 (0.005)	0.090 (0.052)	0.013 (0.005)	0.109 (0.052)
Nematoda	0.001 (0.000)	0.004 (0.001)	0.006 (0.003)	0.008 (0.003)	0.003 (0.001)	0.003 (0.001)
Miscellaneous	0.002 (0.002)	0.015 (0.011)	0	0.001 (0.001)	0	0
Total	1.160 (0.489)	1.699 (0.276)	0.520 (0.207)	0.729 (0.116)	1.114 (0.281)	1.050 (0.277)
			1-4.9 m			
n	9	9	13	13	10	10
Gastropoda	0	0.039 (0.018)	0.287 (0.137)	0.066 (0.022)	0.001 (0.001)	0.104 (0.068)
Bivalvia	0.003 (0.001)	0.015 (0.005)	0.011 (0.004)	0.015 (0.003)	0.009 (0.006)	0.009 (0.005)
Amphipoda	0.004 (0.004)	0.019 (0.010)	0	0.011 (0.005)	0	0.024 (0.016)
Chironomidae-larvae	0.270 (0.092)	0.224 (0.065)	0.370 (0.170)	0.382 (0.218)	0.434 (0.178)	0.652 (0.364)
Chironomidae-pupae	0.010 (0.006)	0.017 (0.009)	0.003 (0.001)	0.004 (0.002)	0.002 (0.002)	0.001 (0.000)
Trichoptera	0	0.015 (0.010)	0.020 (0.012)	0.010 (0.005)	0.006 (0.004)	0.006 (0.002)
Ephemeroptera	0	0.030 (0.025)	0.243 (0.128)	0.071 (0.047)	0.032 (0.018)	0.119 (0.076)
Odonata	0	0.091 (0.091)	0.000 (0.000)	0.001 (0.001)	0	0.292 (0.246)
Ceratopogonidae	0.002 (0.001)	0.011 (0.007)	0.007 (0.002)	0.005 (0.002)	0.005 (0.002)	0.006 (0.003)
Acari	0.002 (0.001)	0	0.001 (0.001)	0	0	0.001 (0.001)
Hirudinea	0.001 (0.001)	0	0	0.002 (0.002)	0	0.007 (0.005)
Coleoptera	0	0	0.001 (0.001)	0.023 (0.016)	0.001 (0.001)	0.004 (0.002)
Oligochaeta	0.046 (0.017)	0.047 (0.035)	0.005 (0.002)	0.036 (0.010)	0.043 (0.020)	0.050 (0.020)
Nematoda	0.001 (0.001)	0.001 (0.001)	0.001	0	0.002 (0.001)	0
Chaoboridae	0.086 (0.031)	0.016 (0.010)	0.005 (0.004)	0.006 (0.005)	0.006 (0.003)	0.039 (0.025)
Miscellaneous	0	0	0	0.010 (0.007)	0	0
Total	0.427 (0.130)	0.525 (0.157)	0.954 (0.240)	0.643 (0.206)	0.541 (0.197)	1.314 (0.474)
			5–9 m			
n	10	13	15	13	15	13
Chironomidae-larvae	0.053 (0.012)	0.123 (0.038)	0.179 (0.028)	0.579 (0.099)	0.104 (0.026)	0.467 (0.097)
Chironomidae-pupae	0	0	0	0	0	0
Ceratopogonidae	0.001 (0.001)	0.001 (0.001)	0	0	0	0
Oligochaeta	0	0.008 (0.007)	0	0.006 (0.003)	0	0.007 (0.003)
Nematoda	0	0	0	0	0	0.019 (0.016)
Chaoboridae	0.076 (0.035)	0.047 (0.024)	0.159 (0.020)	0.228 (0.028)	0.033 (0.004)	0.102 (0.023)
Total	0.130 (0.048)	0.179 (0.071)	0.338 (0.048)	0.813 (0.130)	0.137 (0.030)	0.594 (0.139)

approximately 10 to 50 ng/m^2, with higher values generally found in Ranger Lake. Other taxa that had high Hg pools were the Gastropoda, Odonata, and Ephemeroptera (Table 6).

Fish consumption modeling throughout the summer of 1992 revealed that the monthly transfer of Hg from benthic invertebrates to fishes was consistently higher in Mouse Lake, in comparison with Ranger Lake. The total amount of Hg consumed by all benthivorous fishes from 1 June 1992 to 31 August 1992 was 614.3 and 515.6 µg/ha in Mouse and Ranger lakes, respectively (Figs. 3 and 4). When the consumption rates of Hg were analyzed without the white suckers, the differences between the two lakes were even greater. That is, cumulative Hg consumption for Mouse and Ranger lakes was 356.3 and 132.2 µg/ha, respectively. The consumption rates of Hg by fishes via benthos ranged from 2.3 (July) to 3.6 times higher (August) in Mouse Lake.

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Table 4. Mean individual wet mass (mg) (standard error in parentheses) for Mouse and Ranger Lake Gastropoda, Amphipoda, Chironomidae, Trichoptera, Ephemeroptera, and Odonata from June to August 1992.

Month	Lake	Gastropoda*	*n*	Amphipoda	*n*	Chironomidae*	*n*	Trichoptera	*n*	Ephemeroptera*	*n*	Odonata	*n*
June	Mouse	52.8 (25.4)	4	1.27 (0.05)	14	0.24 (0.01)	25	0.94 (0.2)	6	55.9 (8.5)	9	58.9 (13.4)	11
	Ranger	18.2 (8.9)	19	1.62 (0.1)	19	0.17 (0.01)	25	10.7 (2.9)	14	1.22 (1.07)	12	16.2 (3.7)	16
July	Mouse	60.0 (57.9)	4	0.75 (0.1)	19	0.35 (0.6)	25	1.07 (0.4)	7	7.27 (4.6)	11	18.7 (6.8)	5
	Ranger	5.2 (0.5)	9	0.41 (0.09)	22	0.17 (0.02)	25	1.19 (0.7)	5	1.47 (0.7)	12	29.9 (12.2)	11
August	Mouse	199.1 (124.4)	3	0.60 (0.1)	21	0.39 (0.5)	25	68.3 (39.5)	4	6.2 (5.8)	9	51.2 (22.7)	11
	Ranger	2.2 (0.34)	19	0.46 (0.04)	24	0.01 (0.01)	25	6.8 (5.5)	13	1.88 (1.0)	20	14.5 (4.4)	15

Note: Number of samples = *n*. Significant between-lake differences are indicated by an asterisk (one-way RMANOVA, $p < 0.05$).

Table 5. Total Hg concentrations (ng/g dw) for all benthic invertebrates in Mouse and Ranger lakes, 1992.

Taxon	Mouse	*n*	Ranger	*n*	*p*
Gastropoda	938.7 (92.0)	49	609.9 (53.4)	21	<0.05
Amphipoda	98.2 (22.9)	17	157.6 (20.4)	24	>0.05
Chironomidae (<1 m)	177.2 (18.1)	33	110.3 (9.7)	41	<0.005
Chironomidae (1–4.9 m)	116.4 (9.0)	14	131.1 (19.3)	47	>0.05
Chironomidae (5–9 m)	97.2 (17.1)	36	132.9 (12.4)	33	>0.1
Chaoboridae	73.9 (10.4)	12	82.4 (18.7)	22	>0.05
Trichoptera	92.4 (9.6)	27	70.5 (7.6)	20	>0.05
Ephemeroptera	151.0 (16.2)	15	128.4 (17.2)	12	>0.1
Odonata	135.7 (4.5)	158	112.7 (3.7)	117	<0.001
Ceratopogonidae	162.4 (31.0)	3	99.7 (2.4)	2	>0.1
Coleoptera	—		206.4 (56.0)	9	n/a
Oligochaeta	—		163.7 (2.0)	2	n/a
Miscellaneous	156.7 (18.1)		120.6 (9.7)		n/a

Note: Separate Hg concentrations were obtained for the Chironomidae at each depth interval (i.e., <1, 1–4.9, and 5–9 m). The miscellaneous category represents a combination of rarer taxa (Bivalvia, Coleoptera, Acari, Oligochaeta, and Nematoda in Mouse Lake and Bivalvia, Acari, and Nematoda in Ranger Lake) that individually did not have sufficient biomasses for the Hg analysis. Dashes indicate taxa that were included in miscellaneous benthos. *p*-values from one-way ANOVA between lakes are included, with the exception of some taxa that were not available (n/a).

Discussion

Our results indicate that differences exist in Hg concentrations and Hg pools for benthic invertebrates in lakes with differing fish community structures. The benthic invertebrate Hg concentrations in the lake without piscivores but high numbers of benthivores (Mouse Lake) were generally higher than those in the lake containing piscivores and few benthivores (Ranger Lake), although there were exceptions (i.e., Amphipoda and deeper-water Chironomidae and Chaoboridae). Most noteworthy was the higher total Hg consumption by Mouse Lake fishes via benthos, resulting from their higher consumption rates.

It is not likely that chemical factors influenced the differences in total Hg concentrations in benthic invertebrates between Mouse and Ranger lakes. There were, however, two critical chemical parameters that displayed slight differences and that should be addressed. The epilimnetic pH in Mouse and Ranger lakes was 5.62 and 6.01, respectively, and the alkalinity was 0.28 and 0.62 mequiv./L, respectively.

It is conceivable that the lower levels of pH and alkalinity found in Mouse Lake, factors that are known to enhance Hg levels in fishes (Suns et al. 1987; Spry and Wiener 1991), contributed to the higher Hg concentrations measured in the Mouse Lake benthic invertebrates. However, the same mechanism of enhancing Hg levels in fishes under these conditions cannot explain the differences in Hg concentrations in deeper-water (>1.0 m) benthos between the two lakes. That is, Mouse Lake pH and alkalinity levels were also lower than Ranger Lake values in the deeper zones (i.e., 1.0–4.9 and 5.0–9.0 m) (Ramcharan et al. 1995), yet Hg concentrations in these chironomid larvae (primarily *Chironomus*, the only taxon found at all depth intervals) were not statistically different between the two lakes. In fact, in the deeper-water comparisons, the Ranger Lake chironomid Hg concentrations were slightly higher than in their Mouse Lake equivalents. However, this may only mean that Hg accumulation in chironomids is less sensitive to pH than in other invertebrates.

Although there is evidence that Hg levels in some fishes from localized watersheds are correlated with acidity (e.g., Wren and MacCrimmon 1983; Suns et al. 1987), it has not been established whether Hg concentrations in freshwater invertebrates are actually higher in lakes with lower pH (Wren and Stephenson 1991). Studies on the effects of pH on Hg concentrations in invertebrates are scarce and conflicting. In an experimentally acidified lake, France (1987) found that Hg levels in crayfish abdominal muscles were 0.52 µg/g dw compared with 0.27 µg/g dw in nearby reference lakes. Similarly, in a survey of 13 lakes in southcentral Ontario, 54% of the variability in Hg levels in crayfish abdominal muscles among lakes was explained by conductivity, which was highly correlated

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with lake pH (Allard and Stokes 1989). In contrast, Hg concentrations in composite insect samples from acidified (pH ~ 5.0) and nonacidified (pH ~ 6.5) constructed wetlands were not significantly different (Albers and Camardese 1993). Insects from the composite samples included Coleoptera, Diptera, Ephemeroptera, Hemiptera, Megaloptera, and Odonata. Additionally, a survey of 17 Muskoka area lakes in which pH ranged from 4.8 to 6.4 indicated that Hg concentrations in leeches (*Macrobdella decora* and *Percymoorensis marmoratis*) were not correlated with lake pH (McNicol et al. 1996). In eight remote lakes in Sweden, Hg concentrations in the tissues of some taxa showed an increase with decreasing pH whereas most macroinvertebrates surveyed did not show such a correlation (Parkman and Meili 1993). The scarcity and inconsistency of such data on the effect of pH on Hg concentrations in benthic invertebrates do not allow generalizations to be made with confidence (Campbell and Stokes 1985; Wren and Stephenson 1991).

The positive correlation between dissolved organic carbon (DOC) and Hg accumulation in fishes has received much attention (Suns et al. 1987; Wren et al. 1991). It is believed that humic material (as indicated by DOC concentrations) serves to promote methylation of mercury (Bodaly et al. 1984), and thus, increased humic material will act as an added source of methylmercury (MeHg) in aquatic environments (Mierle 1990). Conversely, Miskimmin et al. (1992) found that increased DOC concentrations led to decreased rates of methylation. The decrease in methylation was believed to be a result of inorganic Hg ions binding with DOC (Miskimmin et al. 1992). Although the effect of DOC on Hg accumulation in invertebrates is not well known (Allard and Stokes 1989), the nearly identical DOC levels in Mouse Lake (4.67 µg/L) and Ranger Lake (4.91 µg/L) preclude the likelihood of this factor contributing to the observed differences in Hg concentrations in the benthos of the two lakes. The similarities in water chemistry are further reflected in the nearly identical total Hg concentrations in the water column and sediments (at all three depth zones) of the two lakes.

Although much attention has been focused on physical and chemical variables in an attempt to explain among-lake variability in contaminant concentrations, relatively little interest has been shown in terms of differences in biotic factors such as food web structure. Some studies have shown that habitat and food selection are important factors in determining Hg concentrations in aquatic invertebrates (Armstrong and Hamilton 1974; Särkkä 1979; Parkman and Meili 1993). This would suggest that food web structure is an important factor in accounting for variability in contaminant concentrations as Hg is biomagnified up the food chain (Armstrong and Hamilton 1974). Although the effect of littoral zone trophic structure on Hg accumulation is not known, it is believed to be significant (Rasmussen et al. 1990).

Although Hg pools were higher in Ranger Lake, Hg concentrations were generally higher in Mouse Lake benthos. The higher Hg concentrations in Mouse Lake benthos were likely a consequence of fishes selectively consuming smaller benthos and leaving the larger benthos. The higher fish populations in Mouse Lake led to stunted growth in fishes in relation to Ranger Lake equivalents (Rocchi 1993; Popiel 1994). Consequently, the fishes in Mouse Lake were precluded from consuming larger prey because of gape limitations. This was corroborated through experimental studies that showed that Mouse lake fishes were less effective at consuming prey because of gape restrictions (N.C. Collins, Department of Zoology, University of Toronto, Toronto, Ont., personal communication).

Fig. 2. Total benthic invertebrate mercury pools for Mouse Lake and Ranger Lake in the depth zones (A) <1.0, (B) 1.0–4.9, and (C) 5.0–9.0 m during June, July, and August 1992. Horizontal lines represent geometric means. Note that the *y*-axis is presented on a log scale. A value of 1 was added to each data point to facilitate plotting of all zero values. Each data point represents a Hg pool value that includes all benthos, based on calculations from the biomass of each sample.

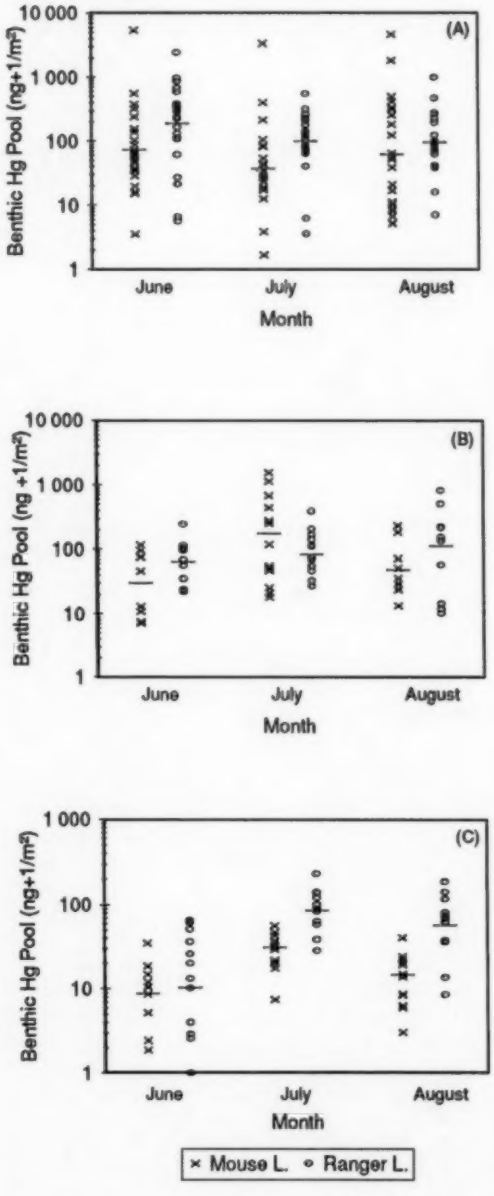

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Table 6. Mean Hg pool (ng/m^2) per taxon and 95% confidence intervals (in parentheses) for benthic invertebrates in all depth zones (i.e., <1.0, 1–4.9, and 5–9 m) of Mouse and Ranger lakes, 1992 (geometric means obtained from back-transformations of logarithmic means (Sokal and Rohlf 1981)).

		Mouse			Ranger		
Month	Taxon	[Hg]	95% CI	*n*	[Hg]	95% CI	*n*
			<1 m				
June	Gastropoda	1.03	(0.00, 3.47)	25	37.47	(13.52, 100.94)	25
	Amphipoda	1.36	(0.57, 2.56)	25	7.75	(3.60, 15.64)	25
	Chironomidae larvae	16.83	(11.30, 24.86)	25	20.28	(13.52, 30.19)	25
	Chironomidae pupae	0.32	(0.03, 0.71)	25	0.70	(0.36, 1.13)	25
	Trichoptera	0.22	(0.01, 0.47)	25	3.34	(1.22, 7.49)	25
	Ephemeroptera	2.90	(0.63, 8.35)	25	0.32	(0.00, 0.84)	25
	Odonata	2.94	(0.72, 8.04)	25	9.80	(3.57, 24.55)	25
	Ceratopogonidae	0.73	(0.37, 1.19)	25	1.02	(0.57, 1.61)	25
July	Gastropoda	1.11	(0.00, 3.67)	25	22.24	(9.56, 50.12)	25
	Amphipoda	0.99	(0.41, 1.82)	25	3.20	(1.79, 5.32)	25
	Chironomidae larvae	8.23	(5.31, 12.50)	25	11.25	(8.30, 15.13)	25
	Chironomidae pupae	0.10	(0.00, 0.21)	25	0.21	(0.04, 0.40)	25
	Trichoptera	0.34	(0.04, 0.71)	25	0.19	(0.00, 0.48)	25
	Ephemeroptera	1.82	(0.42, 4.58)	25	0.92	(0.17, 2.16)	25
	Odonata	1.09	(0.10, 2.96)	25	4.73	(1.54, 11.91)	25
	Ceratopogonidae	0.43	(0.23, 0.67)	25	0.50	(0.24, 0.81)	25
August	Gastropoda	1.15	(0.00, 4.48)	25	10.13	(4.11, 23.27)	25
	Amphipoda	2.02	(1.06, 3.43)	25	4.98	(2.96, 8.03)	25
	Chironomidae larvae	7.45	(5.53, 9.94)	25	6.50	(4.00, 10.25)	25
	Chironomidae pupae	0.09	(0.01, 0.18)	25	0.04	(0.00, 0.10)	25
	Trichoptera	0.55	(0.00, 1.86)	25	0.82	(0.04, 2.18)	25
	Ephemeroptera	0.37	(0.00, 1.16)	25	1.86	(0.53, 4.36)	25
	Odonata	5.34	(1.44, 15.44)	25	4.85	(1.54, 12.50)	25
	Ceratopogonidae	0.16	(0.00, 0.36)	25	0.22	(0.04, 0.43)	25
			1–4.9 m				
June	Gastropoda	0.18	(0.00, 0.71)	9	4.89	(0.27, 26.27)	9
	Amphipoda	0.19	(0.00, 0.77)	9	1.44	(0.12, 4.31)	9
	Chironomidae larvae	14.75	(3.93, 49.36)	9	21.95	(11.63, 40.69)	9
	Chironomidae pupae	0.61	(0.00, 1.71)	9	1.14	(0.08, 3.27)	9
	Trichoptera	0.01	(0.00, 0.04)	9	0.51	(0.00, 1.62)	9
	Ephemeroptera	0.03	(0.00, 0.08)	9	0.85	(0.00, 3.54)	9
	Odonata	0.00	(0.00, 0.01)	9	0.65	(0.00, 4.28)	9
	Ceratopogonidae	0.27	(0.00, 0.67)	9	0.71	(0.07, 1.71)	9
	Chaoboridae	2.88	(0.39, 9.81)	9	0.69	(0.00, 2.08)	9
July	Gastropoda	9.04	(0.48, 67.18)	13	10.35	(2.21, 39.06)	13
	Amphipoda	0.00	(0.00, 0.00)	13	0.92	(0.16, 2.17)	13
	Chironomidae larvae	23.72	(13.04, 42.53)	13	18.30	(7.86, 41.03)	13
	Chironomidae pupae	0.36	(0.15, 0.59)	13	0.38	(0.09, 0.73)	13
	Trichoptera	0.63	(0.00, 1.86)	13	0.39	(0.00, 0.98)	13
	Ephemeroptera	5.94	(1.09, 22.07)	13	2.02	(0.29, 6.07)	13
	Odonata	0.01	(0.00, 0.04)	13	0.10	(0.00, 0.29)	13
	Ceratopogonidae	0.83	(0.35, 1.49)	13	0.41	(0.12, 0.78)	13
	Chaoboridae	0.19	(0.00, 0.57)	13	0.22	(0.00, 0.68)	13
August	Gastropoda	0.29	(0.00, 1.32)	10	7.64	(0.58, 46.36)	10
	Amphipoda	0.00	(0.00, 0.00)	10	0.90	(0.00, 3.62)	10
	Chironomidae larvae	27.79	(12.52, 60.30)	10	26.39	(8.19, 80.62)	10
	Chironomidae pupae	0.18	(0.00, 0.52)	10	0.07	(0.00, 0.17)	10
	Trichoptera	0.34	(0.00, 0.93)	10	0.35	(0.05, 0.73)	10
	Ephemeroptera	1.32	(0.00, 5.06)	10	2.08	(0.00, 9.86)	10
	Odonata	0.00	(0.00, 0.00)	10	2.08	(0.00, 12.12)	10
	Ceratopogonidae	0.61	(0.15, 1.27)	10	0.45	(0.04, 1.01)	10
	Chaoboridae	0.31	(0.00, 0.78)	10	1.27	(0.08, 3.76)	10

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Table 6 (*concluded*).

Month	Taxon	Mouse [Hg]	Mouse 95% CI	Mouse *n*	Ranger [Hg]	Ranger 95% CI	Ranger *n*
			5–9 m				
June	Chironomidae larvae	3.75	(1.57, 7.79)	10	7.57	(2.65, 19.14)	13
	Ceratopogonidae	0.13	(0.00, 0.48)	10	0.08	(0.00, 0.22)	13
	Chaoboridae	3.02	(0.97, 7.24)	10	1.51	(0.29, 3.89)	13
July	Chironomidae larvae	13.98	(8.68, 22.19)	15	57.62	(30.99, 106.41)	13
	Ceratopogonidae	0.00	(0.00, 0.00)	15	0.00	(0.00, 0.00)	13
	Chaoboridae	10.58	(7.95, 13.99)	15	17.27	(13.18, 22.53)	13
August	Chironomidae larvae	6.26	(3.06, 12.00)	15	42.70	(21.68, 83.22)	13
	Ceratopogonidae	0.00	(0.00, 0.00)	15	0.00	(0.00, 0.00)	13
	Chaoboridae	2.25	(1.66, 2.98)	15	5.70	(2.69, 11.17)	13

Fig. 3. Cumulative Hg consumption rates for Mouse Lake (A) yellow perch (YP), pumpkinseed (PKS), and golden shiner (GS) and (B) white sucker (WS) during 1 June to 31 August 1992.

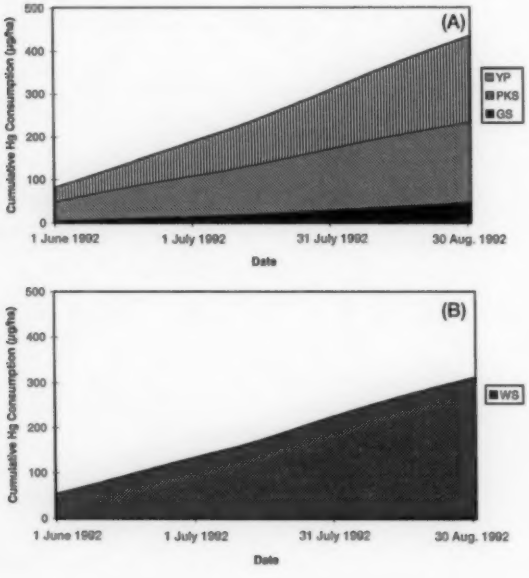
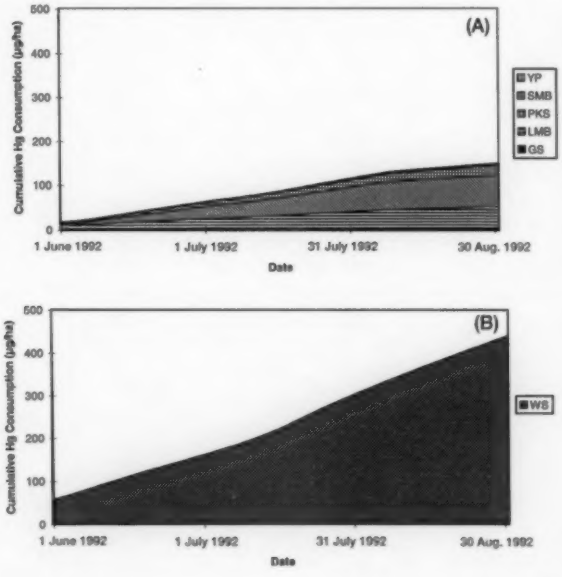


Fig. 4. Cumulative Hg consumption rates for Ranger Lake (A) yellow perch (YP), smallmouth bass (SMB), pumpkinseed (PKS), largemouth bass (LMB), and golden shiner (GS) and (B) white sucker (WS) during 1 June to 31 August 1992.



As a result, individuals in the Mouse Lake benthos were larger and had generally higher Hg concentrations in comparison with those in Ranger Lake. This is in agreement with the positive relationship between Hg concentration and body size found in other aquatic invertebrates (Parkman and Meili 1993). Furthermore, the larger invertebrate predators found in Mouse Lake would likely more often forage on larger prey and thus would be exposed to more Hg because of the biomagnification effect of MeHg (Meili 1991*a*, 1991*b*). Lastly, the Ranger Lake fishes, which had cohorts with larger individuals, were more likely to feed on larger benthic invertebrates, because they are more profitable food items, thus leaving smaller benthos that tend to have smaller Hg concentrations (Morin 1984; Parkman and Meili 1993).

The fraction of MeHg in fishes (~100%) is higher than in benthic invertebrates (Hildebrand et al. 1980; Bloom 1992). Although the fraction of Hg as MeHg in benthos was not measured in the present study, values in similar benthic invertebrate taxa have been reported in other studies ranging from <1 to 100%. Hildebrand et al. (1980) and Huckabee et al. (1979) reported mean percentages of MeHg in benthic invertebrate taxa to be 55 and 76%, respectively, and Parkman and Meili (1993) found that zooplankton had a median value of 65%. Although the fraction of MeHg in invertebrates seems not to be as high as in fishes, it is of foremost importance because it is the form of Hg that biomagnifies up the food chain (Gardner et al. 1978).

Significant ecological impacts of fish predators on benthos have been well documented (Post and Cucin 1984; Keller et al. 1990; Feltmate and Williams 1991). The presence of piscivores in Ranger Lake, coincident with the lower populations of benthivorous fishes, has resulted in lower net predation on the benthos (Wong 1995). This, in turn, has resulted in the

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significantly higher total benthic invertebrate biomass observed in Ranger Lake, as compared with Mouse Lake (Wong 1995). As a consequence, the benthic invertebrate Hg pools were significantly higher in Ranger Lake in comparison with Mouse Lake. This led to total Hg pools in Ranger Lake that were up to 2.7 times higher than in Mouse Lake in the shallow zone and up to 3.9 times higher in the 5.0–9.0 m depth zone.

Despite the higher Hg pools in benthic invertebrates in Ranger Lake, the total Hg consumed by all fish species via benthos was higher in Mouse Lake. The transfer of Hg from benthos to fishes was consistently higher in Mouse Lake. This was attributed to the higher consumption rates by fish in Mouse Lake (Wong 1995). When the consumption rates of Hg were considered without white suckers, the difference was even more evident. In Mouse Lake, the total Hg consumed by fishes via the benthos averaged 2.7 times higher during June –August and was up to 3.6 times higher (August). This was reflected in the higher Hg concentrations found in Mouse Lake fishes (B. Petri, Department of Biology, York University, North York, Ont., personal communication). Omitting white suckers from the analysis of consumption rates by fishes allowed for a more accurate determination of where the differences lie. Although white suckers do consume benthos, they usually were observed at depths >1.0 m in Mouse and Ranger lakes, as in other studies (Tremblay and Magnan 1991; E. Demers, personal observation). Furthermore, the large-bodied white suckers that made up the majority of the white sucker populations in both lakes tended to remain farther offshore (Chen and Harvey 1995). Consequently, differences found in the littoral zone can be attributed to benthivorous fish species other than white suckers. These included yellow perch and pumpkinseed, species that were primarily benthivorous in this study, and in others (Etnier 1971; Sadzikowski and Wallace 1976).

We conclude that a fish community that has a high population of benthivorous species can lead to higher rates of Hg cycling from benthos to fishes, and thus, higher Hg concentrations in fishes. It is these differences in fish trophic structures between lakes that may be a potential source of the variation seen in Hg consumption rates, and thus, Hg concentrations in fishes. Furthermore, differing fish community structures also can affect Hg concentrations and Hg pools in benthic invertebrates as a result of predatory effects. However, because some of the individual invertebrate biomasses and Hg concentrations were not significantly higher in Mouse Lake, predation effects cannot explain all of the differences in Hg concentrations. Our knowledge of metal bioaccumulation in invertebrates is very limited and it is likely that species-specific processes (e.g., uptake and depuration rates) also are acting upon these invertebrate species (Wren and Stephenson 1991). Further research is required to determine the relative importance of this process.

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Juvenile masu salmon (*Oncorhynchus masou*) abundance and stream habitat relationships in northern Japan

Mikio Inoue, Shigeru Nakano, and Futoshi Nakamura

Abstract: Relationships between abundance of juvenile masu salmon (*Oncorhynchus masou*) and stream habitat were analyzed on two spatial scales, stream reach and channel unit, in northern Hokkaido, Japan. Reach-scale analyses revealed that high water temperatures limited the salmon population level and that the salmon abundance increased with cover availability. These two limiting factors were strongly associated with the presence of riparian forest, emphasizing its importance for the salmon population. Channel-unit scale analyses showed greater use of pools by the salmon, with greater depth and abundant cover underlying the patterns of habitat use. However, the relative importance of depth and cover varied among the reach types having different cover availability. In reaches that had abundant cover, cover itself was less important in determining patterns of habitat use within the reaches. In contrast, in reaches with poor cover, patterns of habitat use were strongly affected by cover. The results indicated that habitat characteristics at the reach scale affect not only the salmon abundance of the stream reaches, but also the determinants of local abundance patterns of the salmon within the reaches. It was suggested that larger-scale influences in a hierarchy of habitat scales should be considered for better understanding of fish–habitat relationships.

Résumé : Les relations entre l'abondance d'*Oncorhynchus masou* juvénile et l'habitat de cours d'eau ont été analysées à deux échelles spatiales différentes, tronçon de cours d'eau et unité de chenal, dans le nord d'Hokkaido, au Japon. Les analyses à l'échelle du tronçon ont révélé que la température plus élevée de l'eau limitait l'importance de la population de saumons et que l'abondance des saumons augmentait avec la présence d'un couvert. Ces deux facteurs limitants étaient fortement associés à la présence d'une forêt riveraine, mettant en relief son importance pour la population de saumons. Les analyses à l'échelle de l'unité de chenal ont montré une plus grande utilisation des fosses par les saumons, le mode d'utilisation de l'habitat étant déterminé par la profondeur et l'abondance du couvert. Cependant, l'importance relative de la profondeur et du couvert a varié selon les types de tronçons présentant un couvert différent. Dans les tronçons ayant un couvert abondant, le couvert lui-même était moins important pour déterminer les modes d'utilisation de l'habitat à l'intérieur du tronçon. Au contraire, dans les tronçons ayant un couvert médiocre, les modes d'utilisation de l'habitat étaient fortement affectés par le couvert. Les résultats ont indiqué que les caractéristiques de l'habitat à l'échelle du tronçon influent non seulement sur l'abondance du saumon dans les tronçons du cours d'eau, mais également sur l'abondance locale des saumons à l'intérieur de ces tronçons. Il est proposé que les influences à plus grande échelle dans une hiérarchie des échelles d'habitat soient prises en considération pour mieux comprendre les relations poisson–habitat.
[Traduit par la Rédaction]

Introduction

Habitat characteristics strongly influence populations of stream-dwelling salmonids (Hicks et al. 1991). Thus, fish–habitat relationships provide an ecological basis for stream restoration and management (see Platts and Rinne 1985 and Fausch et al. 1988 for review). In most previous studies, the spatial scales of the research approach varied with the particular interest in question, ranging from watershed to microhabitat levels (see Frissell et al. 1986). However, previous studies have most frequently been conducted at one of three scales: stream reach, channel unit (sensu Grant et al. 1990), or microhabitat.

Reach-scale studies are conducted at the scale of stream reaches in which fish abundance and various habitat variables are measured to examine their relationships. Stream reaches vary in length from tens to several hundred metres and usually include multiple pool-riffle sequences. Many investigators have correlated salmonid abundance with habitat variables (see Fausch et al. 1988 for review), such as water temperature (Bowlby and Roff 1986; Li et al. 1994), pool abundance (Bowlby and Roff 1986; Murphy et al. 1986), cover abundance (Murphy et al. 1986; Wesche et al. 1987), and amount of spawning gravel (Beard and Carline 1991; Bozek and Rahel 1991). This approach helps identify which factors limit fish population levels.

In contrast, both channel-unit- and microhabitat-scale studies focus on identifying the positions that fish adopt within a stream, whether that be in specific habitat types of channel units (e.g., riffles, pools) (Heifetz et al. 1986; Bisson et al.

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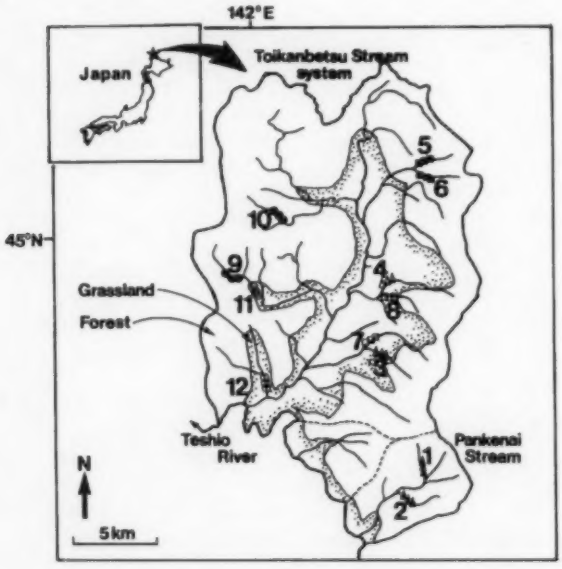

Fig. 1. Location of the study reaches in northern Japan. Solid triangles, coarse-substrate step-pool reach with forest; open triangles, coarse-substrate step-pool reach with grassland; solid squares, coarse-substrate pool-riffle reach with forest; open squares, coarse-substrate pool-riffle reach with grassland; solid circles, fine-substrate pool-riffle reach with forest; open circles, fine-substrate pool-riffle reach with grassland. Numbers correspond to tributaries listed in Table 1.

1988; Nickelson et al. 1992*a*) or as related to microhabitat variables (e.g., depth and velocity measured at the holding positions) (Moyle and Baltz 1985; Heggenes et al. 1991; Bozek and Rahel 1992). Such information is fundamental to habitat improvement techniques (Nickelson et al. 1992*b*; Newbury and Gaboury 1993) and is also important in examining fish–habitat relationships at a larger scale, e.g., the amount of each habitat type is commonly included as a habitat variable of stream reaches (Hubert and Rahel 1989; Larscheid and Hubert 1992).

Most studies on fish–habitat relationships have been designed on only a single scale, but this has not always been sufficient for identifying the factors limiting fish abundance (Bozek and Rahel 1991) because importance of the various factors depends on the scale of the investigations (Crowl and Schnell 1990; Fausch et al. 1994). Thus, multiple-scale investigations are required to better understand fish–habitat relationships (Bozek and Rahel 1991; Fausch et al. 1994). However, the habitat factors detected by the many studies conducted at different spatial scales are site specific (Moyle and Baltz 1985; Fausch et al. 1988; Heggenes et al. 1991; Bozek and Rahel 1992) and possibly reflect larger-scale environmental influences (e.g., climate, landform) peculiar to each study location (Fausch et al. 1988). In turn, patterns of habitat use detected by channel-unit- or microhabitat-scale studies are further affected by the specific characteristics of each stream reach, such as availability of habitat and competitive interactions from various species assemblages (Moyle and Baltz 1985; Heggenes et al. 1991; Bozek and Rahel 1992). Thus, it is important for multiple-scale studies to consider the influences of the larger-scale environment.

Masu salmon (*Oncorhynchus masou*) are distributed around the Asian border of the North Pacific Ocean, are typically anadromous, and have both stream-resident and sea-run type individuals within a population. All masu salmon spawn in headwater tributaries of rivers, and sea-run types may spend several years in small streams before migrating to the sea (Kawanabe 1989). Being largely dependent on freshwater, they are susceptible to the effects of land-use activities, such as logging and agricultural development, that eliminate riparian forests and alter channel geomorphology. This study examined the relationships between juvenile masu salmon abundance and stream habitat using both reach- and channel-unit-scale analyses.

Study area

The study was conducted in tributaries of the Toikanbetsu Stream system and the adjacent Pankenai Stream in northern Hokkaido, Japan (Fig. 1). Both streams flow through the Teshio and Nakagawa Experimental Forests (Hokkaido University) before entering the Teshio River. The western and eastern sides of the main stem of the Toikanbetsu Stream are distinctly different geologically, the western side being underlain by sedimentary rocks and the eastern side dominated by serpentine rocks (Tatewaki and Igarashi 1971). Gentle hillsides extend over much of the area, although the topography of the southeastern part is rather steep. Accordingly, general features of the stream channel differ among the tributaries in the study area. All of the tributaries on the western side are characterized by fine substrate, being low-gradient channels with a regular pattern of pool-riffle sequences associated with bar formation (as described by Sear 1996), whereas streambeds of the eastern side tributaries, which include both low-gradient and high-gradient streams with stepped-bed morphology (sensu Grant et al. 1990), are composed of coarse substrate.

Mixed conifer and deciduous forests originally covered most of the catchments. However, a considerable part of the area has changed to bamboo (*Sasa* spp.) bushlands as a result of several wild fires during the last 100 years (Takaoka and Sasa 1996). Subsequently, the forests and bamboo bushlands around the main stem of the Toikanbetsu Stream were converted to pasture after the 1950's (Ito and Sasa 1993).

Methods

All habitat surveys were conducted when the streams were near their summer base flows during July–October in 1993 and 1994.

Stream reaches of the tributaries were first grouped based on their geomorphological channel features and riparian vegetation. Geomorphological channel features were classified into three types: coarse-substrate step-pool (CSP) and coarse-substrate pool-riffle (CPR) channels on the eastern side and fine-substrate pool-riffle (FPR) channels on the western side. step-pool reaches are distinguished from pool-riffle reaches by the presence of steps, which are formed by channel-spanning accumulations of boulders and cobbles (Bisson and Montgomery 1996). Unlike step-pool reaches, the channel feature of pool-riffle reaches is often sinuous and contains a predictable sequence of pools, riffles, and bars. FPR reaches were poor in coarse substrate materials, such as boulder and cobble, owing to their

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Table 1. General descriptions of the study reaches in 12 tributaries of the Toikanbetsu and Pankenai streams and ranges of elevation, gradient, and mean wetted width for the three study reaches in each tributary.

Number	Tributary	Geomorphological channel type	Riparian vegetation type	Elevation (m)	Gradient (%)	Mean wetted width (m)
1	Pankenai A	CSP	Forest	110–140	3.8–4.2	3.4–3.8
2	Pankenai B	CSP	Forest	70–90	2.5–3.5	2.8–3.1
3	Nuporomaporo A	CSP	Grassland	50–70	2.6–3.3	3.2–3.4
4	Pankerupeshupe A	CSP	Grassland	60–70	2.4–3.2	4.2–5.0
5	Jyuyonsen A	CPR	Forest	70–80	1.6–2.6	2.6–2.9
6	Jyuyonsen B	CPR	Forest	70–80	0.9–1.8	2.1–2.2
7	Nuporomaporo B	CPR	Grassland	40–50	0.8–1.4	3.0–3.4
8	Pankerupeshupe B	CPR	Grassland	40–50	1.0–1.6	1.9–2.5
9	Kenashiporo A	FPR	Forest	50–60	0.5–0.9	2.9–3.5
10	Igarashinosawa	FPR	Forest	60–70	0.5–0.8	3.1–3.4
11	Kenashiporo B	FPR	Grassland	70–80	0.4–0.8	3.1–3.7
12	Nukanan	FPR	Grassland	20–30	0.3–0.7	4.2–5.1

Note: CSP, coarse-substrate step-pool reach; CPR, coarse-substrate pool-riffle reach; FPR, fine-substrate pool-riffle reach. Elevation was determined from 1 : 25 000 topographic maps.

geological characteristics. Riparian vegetation types were classified as either forest, dominated by willows (*Salix* spp.) and an alder (*Alnus hirsuta*), or open grassland of bamboo bushes or pasture. The combination of these features resulted in six reach types (CSP–forest, CSP–grassland, CPR–forest, CPR–grassland, FPR–forest, and FPR–grassland) being recognized for the stream reaches over the study area. We established 36 study reaches on 12 tributaries (three reaches per tributary; Table 1), so that each reach type was represented by six study reaches. Each study reach (50 –160 m in length) consisted of about 10 channel units. All of the study reaches were situated at headwater tributaries (Fig. 1). In addition, the study reaches were not blocked by barriers impassable for fish (e.g., natural waterfalls, artificial dams).

Habitat measurements

A maximum–minimum mercury thermometer was placed in the lowermost study reach of each tributary to record the maximum temperature occurring every 10–14 days during mid-June to late September. Temperatures of the three study reaches within a given tributary were assumed to be the same, owing to their close proximity (within 1 km) and similar riparian vegetation. The gradient of each study reach was measured with a level and leveling rod.

Channel-unit habitat within the study reaches was classified as five types (cascade, rapid, riffle, glide, and pool), according to Bisson et al. (1982). Within each channel unit, four equally spaced transects with five equally spaced measuring points were established. Channel-unit length, wetted width at each transect, and depth at each measuring point were recorded. Substrate type, classified as sand (dominant particle size <2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), and boulder (>256 mm), was recorded at 20-cm intervals along each transect.

Average water velocity of each channel unit was measured by timing the travel of neutrally buoyant balls from the upper to lower end of the channel unit. The celluloid balls (3.6 cm in diameter) were injected with silicon plaster to adjust their specific gravity to nearly equal that of water. Balls were released one by one at 60 equidistant points across the wetted width at the upper end of each channel unit and elapsed time at the lower end for each ball was recorded. Sixty current velocities (centimetres per second) were thereby obtained for each channel unit by dividing the distance traveled (nearest 10 cm) by elapsed time (seconds). The velocity was regarded as 0 cm/s when the ball was retained by an eddy or slack water whereas balls trapped by obstructions (e.g., brush, substrate crevice) were omitted. The average current velocity was expressed as the mean of the 60 velocities and the current complexity as the coefficient of variation for velocity for each channel unit.

Cover is generally considered to be any object that conceals fish from predators or provides shelter from strong current (DeVore and White 1978; Shirvell 1990). Cover was defined as coarse woody debris, brush (often structured by twigs, grass stems, and leaves), undercut banks, and overhanging vegetation (instream or within 40 cm of the water surface). The length and several widths of each cover were measured to calculate the area they occupied within the wetted channel surface.

Other specific features associated with channel geomorphology were not found, e.g., complex off-channel habitats, such as backwater pools and secondary channels, were poorly developed in the study reaches throughout the three geomorphological channel types.

Masu salmon population

The population size of masu salmon was estimated by the removal method of DeLury (1951) during June to early July in 1993 and 1994. In 30 of the 36 study reaches, individual channel units were separately sampled. Each of the other six study reaches (in Pankerupeshupe A and Nukanan) was sampled as a whole, without separating channel units. The population estimate in each of the former 30 study reaches was calculated as the sum of the channel-unit-based estimates for that stream reach.

Each channel unit (or study reach in Pankerupeshupe A and Nukanan) was blocked with 5-mm-mesh seines at the upper and lower ends, and three removal passes were made with an electrofishing unit. The fork length of captured fish was measured and population estimates calculated for parr (age > 0), which could be easily distinguished from fry (age 0) on the basis of their size (the fork lengths of captured parr ranged from 7.7 to 17.1 cm). Fry were not examined in this study. The population estimates were subsequently converted to fish density (per wetted channel area).

Most of the 12 tributaries were commonly inhabited by two benthic fishes (*Noemacheilus barbatulus toni* and *Cottus nozawae*; see Nakano et al. 1995). Two cyprinids (*Tribolodon hakonensis* and *T. ezoe*) were also captured in several tributaries. Two other salmonids (*Hucho perryi* and *Salvelinus leucomaenis*) were found in a few tributaries, but they were rather rare.

Reach-scale analyses

The objectives of the reach-scale analyses were to (1) examine the effects of geomorphological channel features and riparian vegetation on masu salmon abundance and habitat and (2) identify habitat factors limiting masu salmon abundance. Sixteen habitat variables were quantified for the study reaches (hereafter termed reach variable): mean of seven maximum temperatures recorded during mid-June to late September (summer maximum temperature); gradient expressed

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Table 2. Results of two-way ANOVA testing for differences in masu salmon density and reach variables among geomorphological channel and riparian vegetation types.

	Geomorphological channel type (df = 2, 30)		Riparian vegetation type (df = 1, 30)		Geomorphological channel × riparian vegetation (df = 2, 30)	
Variable	*F*	*P*	*F*	*P*	*F*	*P*
Masu salmon density (N/100 m^2)	18.90	<0.001	126.95	<0.001	24.23	<0.001
Summer maximum temperature (°C)	10.09	<0.001	210.99	<0.001	7.90	0.002
Gradient (%)	116.75	<0.001	8.35	0.007	1.08	0.353
Stream width (m)	17.85	<0.001	6.00	0.020	0.66	0.526
Stream depth (cm)	6.61	0.004	23.95	<0.001	2.12	0.138
Area of rapids (%)	8.70	0.001	3.35	0.077	2.20	0.128
Area of riffles (%)	0.12	0.889	4.02	0.054	1.08	0.353
Area of glides (%)	11.83	<0.001	0.19	0.670	0.34	0.717
Area of pools (%)	6.33	0.005	4.36	0.045	4.00	0.030
% sand	8.76	0.001	0.02	0.855	4.39	0.021
% gravel	24.75	<0.001	6.30	0.018	1.97	0.156
% pebble	39.40	<0.001	0.02	0.896	14.47	<0.001
% cobble	29.88	<0.001	0.22	0.645	0.73	0.492
% boulder	190.80	<0.001	18.54	<0.001	10.30	<0.001
Cover area (%)	29.60	<0.001	16.17	<0.001	3.30	0.050

Note: Geomorphological channel types are coarse-substrate step-pool reach, coarse-substrate pool-riffle reach; riparian vegetation types are forest and grassland. Area of cascades and percent bedrock were excluded from the analysis.

as percent change in relative height to reach length (gradient); mean wetted width (stream width); mean depth (stream depth); percentage of overall area of each channel-unit habitat type (area of cascades, rapids, riffles, glides, and pools); relative frequency of each substrate type (percent bedrock, sand, gravel, pebble, cobble, and boulder); percentage of overall area of cover (cover area).

Two-way analysis of variance (ANOVA) was used to examine the effects of geomorphological channel and riparian vegetation types on masu salmon density in the study reaches and on the reach variables. When geomorphological channel effects were significant ($P \leq 0.05$), Tukey–HSD multiple comparisons were subsequently performed. In these analyses, however, area of cascades and percent bedrock were excluded because cascade was absent from pool-riffle reaches, and bedrock was absent from, or contributed very little to, most of the study reaches. Simple univariate regression analysis was used to examine relationships between masu salmon density in the study reaches and each reach variable. All significant variables correlated ($P \leq 0.05$) with masu salmon density were further analyzed by stepwise multiple regression analysis. The reach variables used as independent variables in the multiple regression analysis were not highly correlated with each other ($r = 0.35$–0.71). To standardize variances and improve normality, masu salmon density, stream width, and stream depth were $\log_{10}$-transformed; arcsin transformation was used for areas of channel-unit habitat types, percent substrate types, and cover area.

Channel-unit-scale analyses

Channel-unit-scale analyses were performed to examine (1) habitat use by masu salmon and (2) factors underlying patterns of habitat use. The analyses were conducted separately by geomorphological channel type, but did not include grassland reaches (CSP–grassland, CPR–grassland, and FPR–grassland) because of the very low density of masu salmon there. Six habitat variables were quantified for individual channel units (hereafter termed channel-unit habitat variable): mean depth (depth); current velocity; current complexity; substrate coarseness; substrate heterogeneity; percentage of overall area of cover (cover area). Substrate coarseness and heterogeneity were quantified by the method of Bain et al. (1985) with slight modification. The substrate types were coded in order of coarseness as follows: 1 = bedrock, 2 = sand, 3 = gravel, 4 = pebble, 5 = cobble, and 6 = boulder. The mean coarseness of substrate within each channel unit was used to express substrate coarseness; standard deviation was used to express substrate heterogeneity.

One-way ANOVA and Tukey–HSD multiple comparison tests were used to detect differences in mean masu salmon density among the channel-unit habitat types. Rare channel-unit habitat types ($N \leq 4$; glide in CSP–forest reaches, cascade in CPR–forest and FPR–forest reaches, and rapid in FPR–forest reaches) were excluded from the analyses. Simple univariate regression analysis was used to examine relationships between masu salmon density in the channel units and each channel-unit habitat variable. Variables significantly correlated ($P \leq 0.05$) with masu salmon density were further analyzed by stepwise multiple regression analysis. For these analyses, masu salmon density, depth, current velocity, and current complexity were $\log_{10}$-transformed and cover area arcsin-transformed in order to standardize variances and improve normality. All analyses were performed using SPSS (Norusis 1993).

Results

Reach-scale analyses

Masu salmon density was significantly higher in forest reaches than in grassland reaches across all three geomorphological channel types (Tables 2 and 3). Masu salmon density was also significantly different among geomorphological channel types. Overall the density in CPR reaches was the highest among the geomorphological channel types whereas there was no significant difference between CSP and FPR reaches. Geomorphological channel effects, however, were considered to differ between the forest and grassland reaches owing to the significant interaction effect.

Summer maximum temperatures were significantly different between reaches having different riparian vegetation (Table 2); the temperatures in forest reaches were lower than those in grassland reaches (Table 3). Both geomorphological channel and interaction effects were also significant, reflecting

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Table 3. Mean and SE of masu salmon density and reach variables for each of the six reach types.

	Geomorphological channel and riparian vegetation types					
	Coarse-substrate step-pool		Coarse-substrate pool-riffle		Fine-substrate pool-riffle	
Variable	Forest ($N = 6$)	Grassland ($N = 6$)	Forest ($N = 6$)	Grassland ($N = 6$)	Forest ($N = 6$)	Grassland ($N = 6$)
Masu salmon density (N/100 m^2)	2.5±0.7	0.6±0.2 *b*	20.8±3.1	0.6±0.2 *a*	3.9±0.4	1.40±0.7 *b*
Summer maximum temperature (°C)	16.3±0.2	23.0±0.2 *a*	16.0±0.1	20.0±0.1 *b*	16.1±0.1	20.3±0.1 *b*
Gradient (%)	3.5±0.3	2.9±0.1 *a*	1.7±0.2	1.1±0.1 *b*	0.6±0.1	0.5±0.1 *c*
Stream width (m)	3.4±0.2	3.9±0.3 *a*	2.5±0.1	2.7±0.3 *b*	3.3±0.2	4.0±0.3 *a*
Stream depth (cm)	18.7±1.2	27.9±2.7 *a*	15.8±0.7	20.2±0.5 *b*	18.2±0.5	21.1±1.8 *ab*
Area of cascades (%)	24.5±7.2	8.5±4.3	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Area of rapids (%)	14.7±2.6	31.7±7.2 *a*	11.7±5.3	11.2±4.3 *b*	3.3±1.2	6.5±3.1 *b*
Area of riffles (%)	40.7±7.4	19.7±7.3	34.6±6.3	23.4±5.8	27.8±7.8	26.6±5.6
Area of glides (%)	2.3±2.3	3.0±2.0 *b*	16.9±6.6	15.4±3.3 *a*	23.1±5.8	28.8±6.0 *a*
Area of pools (%)	17.9±4.4	37.2±4.7 *b*	36.9±3.8	50.0±6.0 *a*	45.7±2.6	38.1±6.0 *a*
% bedrock	0.1±0.1	0.0±0.0	0.0±0.0	2.7±2.7	3.0±1.8	2.5±1.5
% sand	4.4±1.3	1.5±0.4 *b*	6.7±1.3	16.7±6.7 *a*	20.5±2.0	12.1±1.2 *a*
% gravel	9.9±1.5	9.0±0.1 *b*	13.8±2.9	9.2±2.3 *b*	31.9 ±3.7	21.0±3.4 *a*
% pebble	17.6±2.6	10.2±1.0 *c*	44.3±5.6	28.0±3.2 *b*	36.9±3.1	57.6±4.4 *a*
% cobble	37.4±2.2	30.7±2.5 *a*	33.4±7.2	36.6±5.4 *a*	7.4±2.4	6.6±0.8 *b*
% boulder	30.6±3.2	48.6±3.4 *a*	1.8±0.9	6.7±1.8 *b*	0.3±0.2	0.1±0.1 *b*
Cover area (%)	0.7±0.5	0.4±0.2 *c*	10.5±1.0	5.4±1.7 *a*	7.0±0.6	3.0±1.0 *b*

Note: Significant differences among geomorphological channel types using two-way ANOVA and Tukey–HSD are denoted by letters: geomorphological channel types followed by the same letter are not significantly different ($P > 0.05$). Area of cascades and percent bedrock were excluded from the analysis.

the high summer maximum temperature in CSP–grassland reaches (Table 3; see also Fig. 2).

Gradient, stream width, and stream depth were significantly different both among geomorphological channel types and between riparian vegetation types (Table 2). The gradient of CSP reaches was the highest followed by those of CPR and FPR reaches; forest reaches had a higher gradient than grassland reaches (Table 3). Both stream width and stream depth were lowest in CPR reaches among the geomorphological channel types; those of forest reaches were less than those of grassland reaches.

The areas of channel-unit habitat types (except for riffle) and percent substrate types were significantly different among geomorphological channel types (Table 2). These results confirmed the initial qualitative classification of the geomorphological channel types. CSP reaches had the largest area of rapids among the geomorphological channel types (Table 3). In contrast, areas of glides and pools were smallest in CSP reaches. Area of pools was also affected by riparian vegetation, but the effects differed among the geomorphological channel types owing to the significant interaction effect (Table 2); mean area of pools was larger in grassland reaches than in forest reaches in both CSP and CPR reaches whereas an opposite trend was found in FPR reaches (Table 3). Percent sand and boulder in CSP reaches were lower and higher, respectively, than in the other geomorphological channel types (Table 3). Although percent gravel and pebble were higher in FPR reaches than in the other geomorphological channel types, FPR reaches had the lowest percentage of cobble. Percent gravel and boulder were also significantly different between riparian vegetation types (Table 2).

Cover area was significantly influenced by both geomorphological channel and riparian vegetation types (Table 2). The cover area in CSP reaches was smaller than that in the other geomorphological channel types, and forest reaches had a larger cover area than grassland reaches (Table 3).

Although many of the reach variables differed both among the geomorphological channel types and between the riparian vegetation types, masu salmon density in the study reaches was significantly correlated with only five of the 16 reach variables based on univariate regressions: summer maximum temperature, stream width, stream depth, percent boulder, and cover area (Table 4). Moreover, stepwise multiple regression analysis revealed that summer maximum temperature and cover area were the best predictors of masu salmon density (Table 5). The lower the summer maximum temperature and larger the cover area characterizing a reach, the higher the density of masu salmon (Fig. 2).

Channel-unit-scale analyses

The mean density of masu salmon was different among the channel-unit habitat types, with pools having the highest density in each of the geomorphological channel types (Table 6). All of the six channel-unit habitat variables were also significantly different among the channel-unit habitat types in any geomorphological channel type (Table 6). Pools were deepest among the channel-unit habitat types, having the lowest current velocity and highest current complexity. In pools, substrate coarseness was also the lowest but substrate heterogeneity the highest. Moreover, cover area in pools was larger than that in the other channel-unit habitat types. These trends were commonly found among geomorphological channel types.

Univariate regressions revealed that channel-unit habitat variables related to masu salmon density in channel units were not always common among the geomorphological channel types (Table 7). The best predictor of the density, detected by stepwise multiple regression analysis for each geomorphological

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Table 4. Results of univariate regression using $\log_{10}$ (masu salmon density + 1) as a dependent variable and each reach variable as an independent variable for the study reaches ($N = 36$).

Independent variable	Regression coefficient	Constant	r^2	F	P
Summer maximum temperature	–0.101	2.402	0.45	28.10	<0.001
Gradient	–0.021	0.566	0.00	0.11	0.736
$\log_{10}$ (stream width)	–2.620	2.167	0.23	10.43	0.003
$\log_{10}$ (stream depth)	–2.887	4.337	0.39	21.92	<0.001
Arcsin (area of cascades)	–0.540	0.561	0.02	0.84	0.365
Arcsin (area of rapids)	–0.643	0.617	0.05	1.63	0.210
Arcsin (area of riffles)	0.558	0.365	0.06	2.01	0.165
Arcsin (area of glides)	0.279	0.488	0.01	0.33	0.569
Arcsin (area of pools)	–0.138	0.584	0.00	0.10	0.760
Arcsin (% bedrock)	–1.539	0.552	0.02	0.59	0.446
Arcsin (% sand)	–0.030	0.534	0.00	0.00	0.967
Arcsin (% gravel)	0.805	0.402	0.04	1.43	0.240
Arcsin (% pebble)	0.515	0.357	0.06	2.09	0.157
Arcsin (% cobble)	0.192	0.481	0.01	0.20	0.659
Arcsin (% boulder)	–0.806	0.653	0.15	5.85	0.021
Arcsin (cover area)	6.723	0.228	0.45	27.38	<0.001

Fig. 2. Masu salmon density in the study reaches in relation to summer maximum temperature and cover area. Solid triangles, coarse-substrate step-pool reach with forest; open triangles, coarse-substrate step-pool reach with grassland; solid squares, coarse-substrate pool-riffle reach with forest; open squares, coarse-substrate pool-riffle reach with grassland; solid circles, fine-substrate pool-riffle reach with forest; open circles, fine-substrate pool-riffle reach with grassland. The axis of masu salmon density is logarithmic scale and that of cover area is arcsin scale.

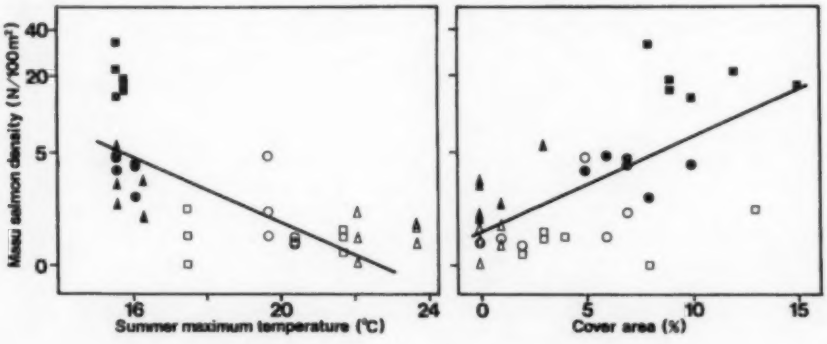

Table 5. Results of stepwise multiple regression analysis using $\log_{10}$ (masu salmon density + 1) as a dependent variable and reach variables as independent variables for the study reaches ($N = 36$).

Independent variable	Regression coefficient	Standard regression coefficient	Model		
			r^2	F	P
Summer maximum temperature	–0.066	–0.44	0.58	23.03	<0.001
Arcsin (cover area)	4.322	0.43			
Constant	1.560				

channel type, was depth or cover area; their relative importance varied with the geomorphological channel type (Table 8; Fig. 3). In CSP reaches, masu salmon density was related to current velocity and cover area on the basis of univariate regressions. However, stepwise multiple regression analysis indicated that only cover area was the best predictor and current velocity was colinear. In CPR reaches, all the variables, except substrate coarseness, were related to masu salmon density on the basis of univariate regressions. However, only depth was significant in the multiple regression analysis. In FPR reaches, all six variables were related to masu salmon density on the basis of univariate regressions. However, the multiple regression model included only depth and cover area as the best predictors of density.

Discussion

Juvenile salmonid abundance in a stream reach is potentially affected by the position of the stream reach in the river system associated with accessibility of adult spawners. However, all of our study reaches were located at similar longitudinal positions. Thus, it can be assumed that our study reaches were equally accessible to adult masu salmon and that juvenile abundance was strongly affected by habitat characteristics of the study reaches. Reach-scale analyses showed that masu salmon density differed both among geomorphological channel types and between riparian vegetation types. Masu salmon

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Table 6. Comparisons of masu salmon density and channel-unit habitat variables among the channel-unit habitat types within each geomorphological channel type by one-way ANOVA and Turkey–HSD tests.

Variable	Channel-unit habitat type					ANOVA results	
	Cascade	Rapid	Riffle	Glide	Pool	*F*	*P*
Coarse-substrate step-pool reach (df = 3, 57)							
Masu salmon density (N/m^2)	0.03±0.01 *xy*	0.01±0.01 *y*	0.02±0.01 *y*		0.07±0.03 *x*	4.01	0.012
Depth (cm)	19.2±0.8 *y*	16.6±1.3 *yz*	15.2±0.7 *z*		25.9±1.4 *x*	18.52	<0.001
Current velocity (cm/s)	32.1±2.3 *xy*	39.8±1.2 *x*	29.2±1.7 *y*		12.0±1.1 *x*	38.58	<0.001
Current complexity[a]	38.1±2.9 *y*	31.6±1.5 *y*	41.9±3.1 *y*		76.7±7.1 *x*	20.99	<0.001
Substrate coarseness[b]	5.1±0.1 *x*	4.9±0.1 *xy*	4.8±0.1 *y*		4.4±0.1 *z*	16.90	<0.001
Substrate heterogencity[c]	1.0±0.1 *y*	0.9±0.1 *y*	0.9±0.0 *y*		1.3±0.1 *x*	10.00	<0.001
Cover area (%)	0.2±0.2 *y*	0.6±0.4 *xy*	0.5±0.4 *y*		3.3±1.4 *x*	4.02	0.012
Coarse-substrate pool-riffle reach (df = 3, 67)							
Masu salmon density (N/m^2)		0.03±0.02 *y*	0.09±0.02 *y*	0.14±0.05 *y*	0.38±0.04 *x*	23.42	<0.001
Depth (cm)		8.0±0.5 *z*	9.0±0.3 *z*	12.7±0.7 *y*	24.5±1.2 *x*	103.19	<0.001
Current velocity (cm/s)		37.7±2.5 *x*	29.9±1.7 *x*	15.1±1.9 *y*	5.1±0.6 *z*	57.67	<0.001
Current complexity[a]		25.2±2.4 *y*	32.1±2.7 *y*	53.7±14.1 *y*	146.0±15.3 *x*	47.90	<0.001
Substrate coarseness[b]		4.5±0.1 *x*	4.4±0.1 *x*	4.1±0.1 *xy*	3.9±0.1 *y*	5.24	0.003
Substrate heterogeneity[c]		0.6±0.1 *y*	0.6±0.0 *y*	0.6±0.0 *y*	0.8±0.0 *x*	15.12	<0.001
Cover area (%)		3.6±1.5 *y*	2.9±0.8 *y*	6.9±1.7 *y*	19.7±1.8 *x*	25.14	<0.001
Fine-substrate pool-riffle reach (df = 2, 55)							
Masu salmon density (N/m^2)			0.00±0.00 *y*	0.01±0.01 *y*	0.08±0.01 *x*	9.99	<0.001
Depth (cm)			0.00±0.4 *y*	13.0±0.7 *y*	26.7±1.5 *x*	78.65	<0.001
Current velocity (cm/s)			36.4±2.4 *x*	22.5±1.5 *y*	8.1±0.9 *z*	85.98	<0.001
Current complexity[a]			28.5±4.9 *y*	33.3±6.1 *y*	98.9±7.1 *x*	52.85	<0.001
Substrate coarseness[b]			3.6±0.1 *x*	3.3±0.1 *y*	3.0±0.1 *y*	7.65	0.001
Substrate heterogeneity[c]			0.7±0.1 *y*	0.8±0.1 *xy*	0.9±0.1 *x*	5.31	0.008
Cover area (%)			3.1±1.1 *y*	6.0±1.8 *y*	11.2±1.4 *x*	9.11	<0.001

Note: Data area means and SE's. Values followed by the same letter are not significantly different ($P > 0.05$). Sample sizes: 14, 10, 25, and 12 for cascade, rapid, riffle, and pool, respectively, in coarse-substrate step-pool reach; 10, 18, 13, and 30 for rapid, riffle, glide, and pool, respectively, in coarse-substrate pool-riffle reach; and 17, 13, and 28 for riffle, glide, and pool, respectively, in fine-substrate pool-riffle reach.

[a]Coefficient of variation (%) of current velocity.

[b]Mean of coded dominant substrate observations.

[c]SD of coded dominant substrate observations.

density in forest reaches was generally higher than that in grassland reaches, with CPR–forest reaches having the highest density. Although various reach variables also differed both among geomorphological channel types and between riparian vegetation types, masu salmon density was best predicted by a combination of summer maximum temperature and cover area. We conclude that masu salmon abundance in the study area was most likely influenced by water temperature and cover; high water temperatures, physiologically stressful to masu salmon, primarily limited their population level, and in the streams free from such thermal stress, the population level increased with cover abundance.

Masu salmon density was lower in the reaches of higher summer maximum temperature. Average summer maximum temperature in grassland reaches was approximately 5°C higher than that in forest reaches (Table 3), although stream temperature is potentially influenced by elevation and stream width as well as riparian canopy. The average elevation of the forest reaches was approximately 30 m higher (Table 1), with the average width 0.5 m smaller (Table 3) than that of the grassland reaches. Nevertheless, these differences cannot account for these temperature differences, according to Sugimoto et al. (1995), who examined factors influencing spatial variation in stream temperatures in the Toikanbetsu Stream system. Thus, the absence of riparian canopy, which intercepts much of the solar radiation over small forest streams (Brown and Krygier 1970; Nakamura and Dokai 1989), was the most likely cause of high stream temperatures in the grassland reaches. The upper thermal tolerance for active feeding and growth of juvenile masu salmon is 18°C with the preferred range being 8–15°C (Mayama 1992). Summer maximum temperatures in many of the grassland reaches were greater than 20°C, and therefore could be physiologically stressful to masu salmon.

Cover also influenced masu salmon density. Previous reach-scale studies have demonstrated similar positive relationships between cover and salmonid abundance (Murphy et al. 1986; Wesche et al. 1987), with cover being believed to enhance the carrying capacity of streams (DeVore and White 1978; McMahon and Hartman 1989). These findings are supported by many channel-unit- or microhabitat-scale studies, which have shown strong preference for cover by salmonids (Fausch and White 1981; Cunjak and Green 1983; Heifetz et al. 1986; Shirvell 1990; Fausch 1993). Cover can allow fish to hold a profitable position of low water velocity adjacent to a swift current. It also reduces predation risk by decreasing visibility and increasing visual isolation, which can reduce interference interactions (Fausch 1993).

Cover abundance in our study reaches was influenced by geomorphological channel features as well as riparian vegetation.

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Table 7. Results of univariate regression analysis using $\log_{10}$ (masu salmon density + 1) as a dependent variable and each channel-unit habitat variable as an independent variable for the channel units within each geomorphological channel type with forest.

Independent variable	Regression coefficient	Constant	r^2	F	P
Coarse-substrate step-pool reach (N = 63)					
$\log_{10}$ (depth)	0.033	–0.030	0.03	2.29	0.135
$\log_{10}$ (current velocity + 1)	–0.031	0.050	0.10	6.99	0.010
$\log_{10}$ (current complexity + 1)	–0.023	–0.026	0.04	2.36	0.130
Substrate coarseness	–0.017	0.023	0.00	0.06	0.814
Substrate heterogeneity	0.030	0.003	0.01	0.35	0.556
Arcsin(cover area)	0.416	0.007	0.30	26.46	<0.001
Coarse-substrate pool-riffle reach (N = 71)					
$\log_{10}$ (depth)	0.235	–0.201	0.48	63.20	<0.001
$\log_{10}$ (current velocity + 1)	–0.098	0.186	0.36	38.03	<0.001
$\log_{10}$ (current complexity + 1)	0.119	–0.132	0.36	38.82	<0.001
Substrate coarseness	–0.254	0.232	0.04	2.72	0.103
Substrate heterogeneity	0.547	–0.047	0.15	12.15	0.001
Arcsin(cover rate)	0.380	0.035	0.33	33.92	<0.001
Fine-substrate step-pool reach (N = 62)					
$\log_{10}$ (depth)	0.075	–0.077	0.36	34.23	<0.001
$\log_{10}$ (current velocity + 1)	–0.036	0.060	0.25	20.06	<0.001
$\log_{10}$ (current complexity + 1)	0.033	–0.039	0.18	13.65	<0.001
Substrate coarseness	–0.122	0.078	0.10	6.81	0.011
Substrate heterogeneity	0.121	–0.014	0.09	5.74	0.020
Arcsin(cover area)	0.187	0.002	0.29	24.38	<0.001

Table 8. Results of stepwise multiple regression analysis using $\log_{10}$ (masu salmon density + 1) as a dependent variable and channel-unit habitat variables as independent variables for the channel units within each geomorphological channel type with forest.

Independent variable	Regression coefficient	Standard regression coefficient	Model r^2	Model F	Model P
Coarse-substrate step-pool reach (N = 63)					
Arcsin(cover area)	0.416	0.55	0.30	26.46	<0.001
Constant	0.007				
Coarse-substrate pool-riffle reach (N = 71)					
$\log_{10}$ (depth)	0.235	0.69	0.48	63.20	<0.001
Constant	0.201				
Fine-substrate pool-riffle reach (N = 62)					
$\log_{10}$ (depth)	0.056	0.45	0.43	23.12	<0.001
Arcsin(cover area)	0.110	0.32			
Constant	0.061				

Riparian forests supply various cover materials (e.g., woody debris, brush, and overhanging vegetation), in addition to stabilizing undercut banks with woody roots (Beschta and Platts 1986; Bisson et al. 1987). The low abundance of cover in CSP reaches can be attributed to high stream power that can transport such cover materials.

These results emphasize the importance of riparian forest in maintaining suitable thermal conditions and providing habitat components for juvenile masu salmon. The effects of riparian vegetation on salmonids have been well investigated in North America, especially in the Pacific Northwest. These studies have shown that removal of riparian forest can have both positive and negative effects on salmonid populations. Enhancement of food resources (benthos) associated with increased primary production is a positive effect (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983; Johnson et al. 1986; Murphy et al. 1986; Bilby and Bisson 1992) whereas reduction of habitat space (e.g., pool volume) created by woody debris is negative (Tschaplinski and Hartman 1983; Heifetz et al. 1986; Johnson et al. 1986; Murphy et al. 1986). In addition, the relative intensities of these effects depend on season and life stage of the fish (Johnson et al. 1986; Murphy et al. 1986).

In the above studies, increased water temperatures resulting from canopy removal were still within thermal tolerance ranges for salmonids, apparently due to either the cool climate of the region or the small area of canopy removed. Thus, resident fish could receive the benefits of increased food availability, without additional thermal stress, in those streams (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983; Bilby and Bisson 1992). However, even if enhancement of food resources had occurred in the grassland reaches of our study area, the benefits would be masked by the thermal limitations. Similar cases of salmonids being thermally limited have been reported in some other regions of North America (Barton et al. 1985; Li et al. 1994). Elimination of riparian forests in northern Hokkaido, Japan, is expected to result in a negative effect overall on resident masu salmon populations.

In the Pacific Northwest, streams with riparian forest generally have greater pool abundance than those without riparian forest (Heifetz et al. 1986; Murphy et al. 1986; Bilby and Bisson 1992; Ralph et al. 1994). However, this trend was not seen in the present study, probably due to differences in riparian tree size. Large old-growth conifers dominate riparian forests in the Pacific Northwest whereas the riparian forests in the present study area were dominated by relatively small deciduous

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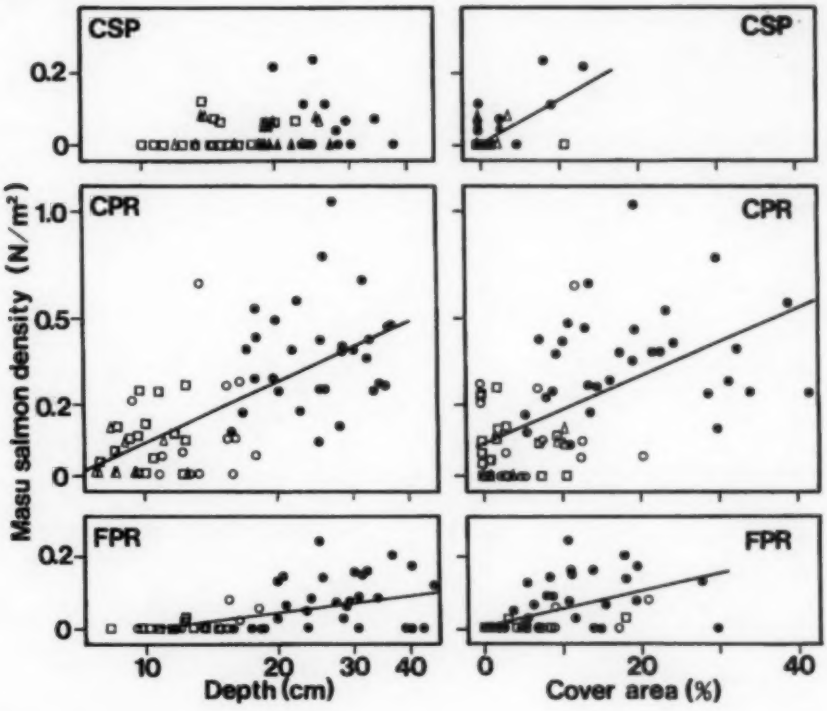
Fig. 3. Masu salmon density in relation to depth and cover area in the channel units within each geomorphological channel type with forest. CSP, coarse-substrate step-pool reach; CPR, coarse-substrate pool-riffle reach; FPR, fine-substrate pool-riffle reach. Solid triangles, cascade; open triangles, rapid; open squares, riffle; open circles, glide; solid circles, pool. The axes of masu salmon density and depth are logarithmic scale and that of cover area is arcsin scale.



trees (<40 cm diameter at breast height, <20 m height), such as willows and an alder. Although woody debris from the old-growth coniferous forests can create pools or increase individual pool volume (Bisson et al. 1987; Andrus et al. 1988; Robison and Beschta 1990), that from the deciduous forests in our study area is probably insufficient to have such an effect.

In the present study, effects of larger reach-scale habitat characteristics were clearly recognizable in the fish–habitat relationships at the smaller channel-unit scale. Channel-unit scale analyses showed differential use of channel-unit habitat types by masu salmon, and the best predictors of the patterns of habitat use, as revealed by the multiple regression analyses, differed among geomorphological channel types. In CSP reaches that had very little cover abundance, the pattern of habitat use was best explained by cover area whereas in CPR reaches, which were shallow but had abundant cover, depth was the best predictor. In FPR reaches with moderate cover abundance, the pattern of habitat use was best explained by a combination of depth and cover area. In these cases, reaches that had abundant cover could support high densities of masu salmon, although cover itself was less important in determining local abundance patterns of masu salmon within the reaches. In contrast, in reaches with poor cover where masu salmon density was low, local abundance patterns were strongly affected by cover.

Pools appear to provide important habitat for masu salmon, having considerable depth and abundant cover, based on channel-unit-scale analyses. Greater use of pools has been documented for masu salmon (Inoue and Nakano 1994; Nakano 1995) and other salmonids in studies at the channel-unit or microhabitat scale (Bisson et al. 1988; Heggenes et al. 1991; Nickelson et al. 1992*a*). Moreover, several reach-scale studies have shown positive relationships between pool abundance and salmonid abundance (Bowlby and Roff 1986; Murphy et al. 1986; Fausch and Northcote 1992). The present reach-scale analyses, however, did not indicate that pool abundance was a limiting factor for populations of masu salmon, suggesting that pool quality, rather than quantity, was more important. The carrying capacity of a pool can be enhanced by the presence of cover, which in turn can provide suitable microhabitat space in non-pool units.

Although these types of analyses on observational patterns give relatively little insight into detailed mechanisms underlying the patterns (Fausch 1993), they provide an important framework for future studies for elucidating mechanisms (Crowl and Schnell 1990). Our analyses indicated that the importance of factors varies according to the scale, as pointed out by some previous multiple-scale studies (Crowl and Schnell 1990; Bozek and Rahel 1991; Fausch et al. 1994). Moreover, fish–habitat relationships detected at a small scale can be influenced by the larger-scale environment. For example, our reach-scale results differed from those in the Pacific Northwest (e.g., Murphy et al. 1986) due to some region-specific conditions. In addition, results of the channel-unit-scale analyses

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differed among geomorphological channel types under the influence of stream-reach characteristics. These results emphasize the necessity of considering the effects of larger-scale environment in a hierarchy of habitat scales to improve general understanding and sound management of stream ecosystems.

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Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship

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Abstract: We examined the diet of Steller sea lions (*Eumetopias jubatus*) during June–August 1990–1993 from six areas in the Aleutian Islands and Gulf of Alaska and related these diets to sea lion population changes that occurred during the period. Seven general prey categories were identified, but either walleye pollock (*Theragra chalcogramma*) or Atka mackerel (*Pleurogrammus monopterygius*) dominated in every area. The diversity of prey consumed varied among sites. Only the eastern Aleutian Islands area had all seven categories in the diet, and there, walleye pollock and Atka mackerel each made up around 30% of the diet. The remainder was composed mostly of small schooling fish (e.g., Pacific herring (*Clupea pallasi*) and salmon (*Oncorhynchus* spp.)). The diet in the Gulf of Alaska included mostly walleye pollock whereas the central and western Aleutian diet was composed mostly of Atka mackerel. Populations in the six areas decreased up to 49% during 1990–1994. A strong positive correlation ($r = 0.949$, $P = 0.004$) was found between diet diversity and the amount of decline in an area: as diet diversity decreased, populations decreased. This suggests that sea lions need a variety of prey available, perhaps to buffer significant changes in abundance of any single prey.

Résumé : Nous avons examiné le régime alimentaire de l'otarie de Steller (*Eumetopias jubatus*) entre juin et août de 1990 à 1993 dans six régions des îles Aléoutiennes et du golfe de l'Alaska et relié ces régimes alimentaires aux changements de la population d'otaries observés durant cette période. Sept catégories générales de proies ont été observées, mais dans toutes les régions, les proies ont été dominées soit par la goberge de l'Alaska (*Theragra chalcogramma*) ou maquereau Atka (*Pleurogrammus monopterygius*). La diversité des proies consommées a varié d'un site à l'autre. Seules les otaries de la région des îles Aléoutiennes orientales comptaient les sept catégories dans le régime alimentaire, et à cet endroit, la goberge de l'Alaska et maquereau Atka constituaient chacun environ 30% du régime alimentaire. Le reste était constitué surtout de petits poissons vivant en bancs (p. ex., harengs du Pacifique (*Clupea pallasi*) et saumons (*Oncorhynchus* spp.). Dans le golfe de l'Alaska, le régime alimentaire était constitué surtout de goberges de l'Alaska, alors que dans les régions centrales et occidentales des Aléoutiennes, c'était maquereau Atka. Les populations dans les six régions ont diminué d'une valeur allant jusqu'à 49% au cours de la période 1990–1994. Une forte corrélation positive ($r = 0{,}949$, $P = 0{,}004$) a été observée entre la diversité du régime alimentaire et l'importance du déclin dans une région : lorsque la diversité du régime diminue, la population en fait autant. Cette constatation indique que l'otarie doit avoir à sa disposition une variété de proies, peut-être pour pouvoir absorber les variations importantes d'abondance qui touchent les proies individuelles.
[Traduit par la Rédaction]

Introduction

The cause(s) of the 68% decline in the U.S. population of Steller sea lions (*Eumetopias jubatus*) since the 1970s remains uncertain (National Marine Fisheries Service (NMFS) 1995); however, the consensus among researchers appears to be that the decline is a result of changes in the availability of preferred prey (Merrick et al. 1987; D. Calkins, Alaska Department of Fish and Game (ADF&G), 333 Raspberry Rd., Anchorage, AK 99502, unpublished data; Loughlin and Merrick 1989; Alverson 1991; Springer 1992; Alaska Sea Grant 1993).

Examination of the health of individual animals as a means of evaluating the food limitation hypothesis has provided inconclusive results. Kodiak Island area sea lions were significantly shorter and lighter in 1985–1986 (during the decline) than they were in 1975–1978 (before the decline had begun) (D. Calkins, unpublished data). However, current studies of sea lion condition and health have found no significant differences between adult females and pups in summer in the Gulf of Alaska (a declining population) and southeast Alaska (an increasing population) (Castellini 1993; Davis et al. 1993; Rea et al. 1993; Spraker et al. 1993; Merrick et al. 1995; Rea 1995). Despite the apparent disappearance of thousands of sea lions each year, it has not been possible to evaluate the cause of the decline from beach-cast animals because few dead animals have been found.

An alternative approach to evaluating the food limitation hypothesis is to compare food habits between areas of the range with different population trajectories. To facilitate such analyses, the NMFS, ADF&G, and U.S. Fish and Wildlife Service (USF&WS) began a diet sampling program for Steller sea lions in 1990 that encompassed most of the region of decline in Alaska, from the Kenai Peninsula to the western Aleutian Islands. Declines continued in this region during the period, although the rates of change differed among areas (from +1 to –49%; Strick et al. 1997). Here, we present an

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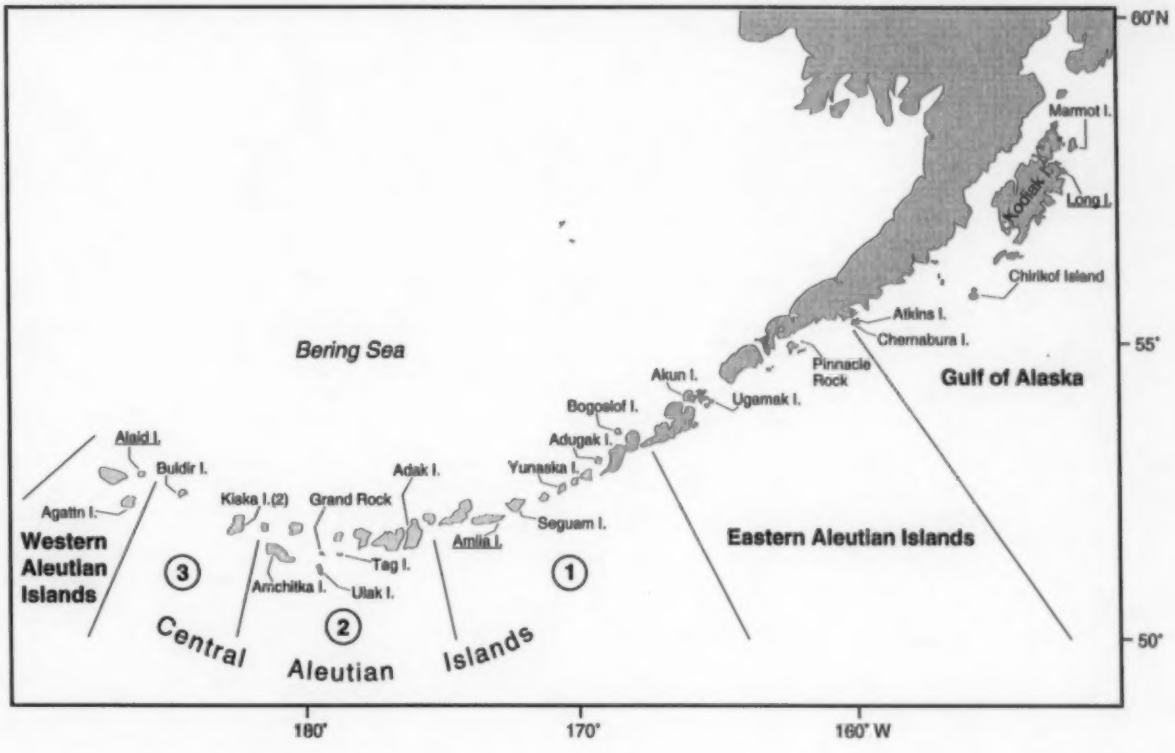
Fig. 1. Sites and diet analysis areas in Alaska where Steller sea lion fecal samples were collected for 1990–1993. Haul-outs are underlined and include Long, Amlia, and Alaid islands. All remaining sites are rookeries, with Kiska Island including two separate rookeries.



area-specific comparison between diet and population change. We initially tested a hypothesis of no difference in diets between areas (i.e., no relationship between diet and rates of declines). Differences were found; thus, we tested a second hypothesis that there was no relationship between diet and the amount of decline by area. Rejection of this hypothesis would then support a third hypothesis that diet and the decline were related.

Materials and methods

Collection and laboratory methods

Fecal samples ($n = 421$) were collected at Steller sea lion haul-outs and rookeries during the last week of June and first week of July or the first week of August (western Aleutian Islands only) of 1990–1993. A total of 37 collections were made at 19 rookeries and three haul-outs in the area from the Kodiak Archipelago in the central Gulf of Alaska westward through the Near Islands in the western Aleutian Islands (Fig. 1). Most of the sea lions (other than pups) on the rookeries were adult females, so most of the scats collected came from adult females.

Biologists collected only fresh scats to ensure that remains were from recent feeding trips. Older scats are harder to process, and could result in damaged hard parts. A scat was only collected if it was obvious that it had come from one animal. Each scat was scooped into a separate gallon-sized plastic bag and frozen. Scats were processed at the National Marine Mammal Laboratory's food habits laboratory in Seattle, Wash.. Samples were thawed and allowed to soak for at least 24 h in an emulsification mixture (Treacy and Crawford 1981) or until the scat had softened and formed a slurry at the bottom of the bag. The softened scat materials were either hand-washed through a series of three nested sieves (2, 1, and 0.5 mm) or passed through an automated washing device (an elutriator; Bigg and Olesiuk 1990) to separate the prey materials. Identifiable hard parts (otoliths, other intact bones, teeth, and beaks) were removed and stored dry in vials. Prey remains contained in each scat were identified by comparing them with reference materials. Most of this identification was performed by Pacific Identifications, Victoria, B.C. Prey were identified to the lowest taxonomic level possible (often species) using multiple structures. A detailed discussion of these methods is provided in Olesiuk et al. (1990). Of the original 421 scats, 364 contained identifiable fish or cephalopod remains (Merrick 1995), 39 contained only unidentifiable fish parts, and 18 contained no identifiable remains. Taxa identified from the 364 scats were grouped into the following categories: (1) gadids: walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), and unidentified gadids; (2) Pacific salmon (*Oncorhynchus* spp.); (3) small schooling fish: capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasi*), eulachon (*Thaleichthys pacificus*), and Pacific sand lance (*Ammodytes hexapterus*); (4) flatfish: arrowtooth flounder (*Atheresthes stomias*), rock sole (*Pleuronectes bilineatus*), and other pleuronectids; (5) other demersal fish: sculpins (Cottidae), rockfish (*Sebastes* spp.), Stichaeidae, skates (*Raja* spp.), sharks, and lamprey (*Lampetra* sp.); (6) Atka mackerel (*Pleurogrammus monopterygius*); (7) cephalopods: squid and octopus. Species were grouped based on similarities in their behavior (e.g., schooling versus nonschooling), nutritional content, and patterns of abundance during the period (Merrick 1995). Analysis at a higher taxonomic level also reduces the effect of errors in the identification of prey.

Analyses

Separate analysis of the 37 individual collections (a day and site

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combination) was generally inappropriate because of the small sample size and because of biases possible from site- and time-specific samples. We were concerned about sample sizes, from 1 to 22 scats per collection with a mean of 10, because unrepresentative small samples (e.g., a collection of one scat) could inadvertently skew the results. Thus, we dropped from analysis the nine collections with less than five scats (a total of 26 scats). This left 338 scats for analysis. Furthermore, we expected that because each collection only reflected what was available at the site on the collection day, individual collections were not accurate indices of the general diet of the site or area. Collections should probably be viewed as a sampling unit. Consequently, we decided that it would be more appropriate to use some aggregation of collections.

Adjacent sea lion rookeries have had similar population trends (York et al. 1996), suggesting that some shared environmental feature (e.g., a common food resource) might link sites together. Because our research focused on associating population change with dietary differences, an analysis structure that captured this spatial pattern of common population trends seemed appropriate. Therefore, we used a spatial structure developed from a cluster analysis of individual rookery population trends from 1989 to 1994 (York et al. 1996): (*i*) Gulf of Alaska (GOA); (*ii*) eastern Aleutian Islands (EAI); (*iii*) central Aleutian Islands Area 1 (CAI-1); (*iv*) central Aleutian Islands Area 2 (CAI-2); (*v*) central Aleutian Islands Area 3 (CAI-3); (*vi*) western Aleutian Islands (WAI). This geographical structure (Fig. 1) was used for the food habits analyses discussed here.

Calculation of the frequency of occurrence of prey categories within the diet

The relative importance of prey in the diet was measured using split-sample frequency of occurrence (Olesiuk et al. 1990). The split-sample frequency of occurrence of each prey category (FO_{jk}) for a collection was calculated as follows:

$$FO_{jk} = \sum_{i=1}^{n_j} (O_{ijk} / \sum_{k=1}^{7} O_{ijk}) / n_j$$

where i = scat sample within a collection, j = collection (each site and year combination), k = prey categories ($1 \geq k \geq 7$), and O_{ijk} = a binary variable for the presence of prey category k in the ith scat sample for area j. Thus, the frequency of occurrence (FO_{jk}) in the diet of the kth prey categories in the jth collection was estimated from the $i = 1$ to n_j samples collected in that analysis area. The FO_{ak} for a specific category (k) for an analysis area (a) was calculated as the sum of the weighted category FOs for all j collections from the area:

$$FO_{ak} = \sum_{j=1}^{n_a} [FO_{jk} \cdot (p_j / P_a)]$$

where p_j = number of animals counted at the site around the time of the collection, P_a = total number of animals counted at all analysis area sites where collections occurred, and n_a = number of collections in an analysis area. Population numbers used in the weighting were obtained from the NMFS aerial survey typically conducted 2–3 weeks prior to the date of the collection.

The split-sample approach assumes that remains in the sample represent a complete sample of all prey consumed in the most recent meal(s) and that individual prey taxa were consumed in the meal in equal volume. Olesiuk et al. (1990) assessed the degree to which these assumptions were violated using dietary information from the northern fur seal and found the amount of error to be relatively small. However, in viewing these results, one must remain aware that certain fish with small bony structures may be underrepresented. A volumetric approach would have been preferable; however, the requisite data for volumetric analyses (e.g., otoliths to estimate prey size) usually are not available from Steller sea lion scats.

Diet diversity index (DDI)

An index was developed using the Shannon–Wiener species diversity index (Ricklefs 1979) as a model to evaluate diet differences between analysis areas:

$$DDI_a = e^{-\sum_{k=1}^{7} FO_{ak} \ln FO_{ak}}$$

where DDI_a = diversity of the ath area. Potential values ranged from 1.0 (one taxon in the diet) to 7.0 (all seven categories equally represented). Analysis area DDI_a were calculated from the mean FO_{ak} values for all collections within the area.

Analysis of spatial and temporal differences

Techniques for statistical comparisons of the split-sample FO values have not been rigorously developed. Therefore, we used a contingency table analysis of the numerical occurrence of prey categories in scats (Pearson χ^2, $\alpha = 0.05$) to test for spatial differences.

Temporal differences were analyzed for two areas: the eastern Aleutian Islands and the Kodiak Island area of the Gulf of Alaska. For the eastern Aleutian Islands, diet samples were available from Bogoslof and Ugamak islands for 1985–1989 (40 scats) and 1990–1993 (52 scats). Comparisons in the Kodiak Island area were made between the June–July stomach collections from 1976–1978 (n = 28) and 1985–1986 (n = 20) and the 1990–1993 scat collections (n = 54) (Pitcher 1981; D. Calkins, unpublished data; Merrick and Calkins 1996). Because the Kodiak collections from the 1970s and 1980s were from stomachs with prey identified only from whole fish or from otoliths, it is likely that the results are not strictly comparable with the 1990–1993 scat analyses. To minimize the effect of these differences on comparisons, only the proportions of animals consuming a prey category group were compared (rather than attempting to calculate a split-sample frequency of occurrence). Contingency table (Pearson χ^2, $\alpha = 0.05$) analysis was used to test the frequency of occurrence of each of the seven categories by time or area.

Comparison between diets and population change

The DDI and FO (by category) were compared (correlation coefficients, $\alpha = 0.05$) with the estimated population change of an analysis area's rookery population for the period from 1990 to 1994. Count data were obtained from the 1990 and 1994 NMFS Steller sea lion aerial surveys (Merrick et al. 1991; Strick et al. 1997). No survey occurred in 1993.

Results

The 338 scats with identifiable contents contained the remains of 29 taxonomic groups, including 13 species (Merrick 1995). Atka mackerel was the most common prey category and species identified (209 occurrences in the 338 samples). Gadids, the second most common taxon (n = 145 scats), included 98 scats with walleye pollock, 95 with unidentified gadids (probably walleye pollock), six with Pacific cod, and five with Pacific hake. Salmon and cephalopods were the third (n = 66 scats) and fourth (n = 39 scats) most common prey. Cephalopods were always found in association with fish remains. Thirty samples included small schooling fish. In almost all cases, these scats contained only small schooling fish remains; therefore, they were not introduced from the guts of other larger fish (e.g., Pacific cod or walleye pollock). Most of the small schooling fish were Pacific herring (n = 16 scats) or Pacific sand lance (n = 11 scats), but capelin (n = 3 scats) and eulachon (n = 1 scat) were also found. Other demersal fish were found in 22 samples and included a variety of species. Flatfish was the least commonly found category (n = 11 scats).

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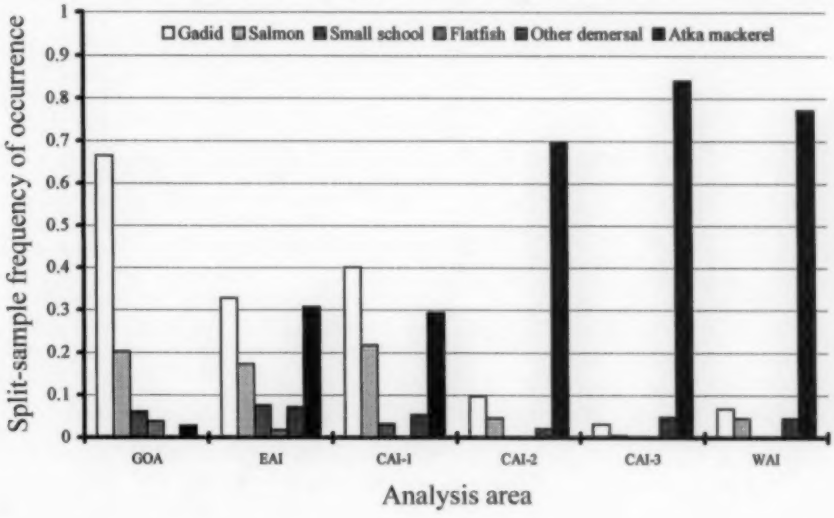
Table 1. Steller sea lion's relative consumption of seven prey categories, DDI, and percent decline in rookery populations by area of Alaska (see Fig. 1 for analysis areas) for 1990–1993.

Area	Sample size[a]	Gadids (%)	Salmon (%)	Small schooling (%)	Flatfish (%)	Other demersal (%)	Atka mackerel (%)	Squid or octopus (%)	DDI	Decline 1990–1994 (%)
Gulf of Alaska	76 (8)	66.5	20.3	6.1	3.9	0.0	0.3	2.9	2.8	–35.7
EAI	67 (5)	32.9	17.3	7.7	1.8	7.3	30.7	2.3	4.0	1.1
CAI-1	33 (3)	40.2	21.8	3.3	0.0	5.4	29.4	0.0	3.2	–20.1
CAI-2	54 (5)	9.7	4.7	0.0	0.0	2.2	69.7	13.7	2.5	–25.2
CAI-3	80 (4)	3.2	0.5	0.0	0.0	4.9	84.2	7.1	1.6	–48.5
WAI	28 (2)	6.9	4.6	0.0	0.0	4.6	77.3	6.7	2.0	–40.9
Area-wide	338 (27)	25.6	11.1	3.1	0.7	3.3	50.7	5.4	3.5	–20.7
Pearson χ^2		130.3	38.3	55.9	19.0	18.5	186.2	27.7		
P		<0.001	<0.001	<0.001	0.002	0.002	<0.001	<0.001		

Note: Pearson χ^2 calculated from the number of scats with or without a prey.
[a]Number of collections in parentheses.

Fig. 2. Proportion of Steller sea lion diet attributable to six fish prey categories by Alaskan analysis area from 1990–1993 fecal samples.



Spatial differences

All seven categories had different (Pearson χ^2, $P < 0.01$) spatial consumption patterns (Table 1). Diet in each area was dominated by one or two categories (walleye pollock or Atka mackerel; Fig. 2); however, there was a distinct shift in the dominant taxon from east to west. The major prey of sea lions in the Gulf of Alaska was walleye pollock (FO = 0.665). The proportion of walleye pollock in the diet decreased to the west where it was replaced by Atka mackerel (Fig. 2). From Area 2 in the central Aleutian Islands westward the diet consisted mostly of Atka mackerel (FO = 0.647–0.842). Salmon, small schooling fish, and flatfish were found more commonly in the eastern areas. No spatial patterns were apparent for other demersal fish or cephalopods.

Only the eastern Aleutian Islands scats contained all seven categories (Table 1). Atka mackerel and walleye pollock made up roughly equal parts of the diet. This area had the highest proportion of small schooling fish and other demersal fish, and a moderately high proportion of salmon. Area 3 of the central Aleutian Islands represented the opposite dietary extreme. It had the highest proportion of Atka mackerel in the diet and the lowest proportions of gadids, salmon, small schooling fish, and flatfish in the diet.

Differences existed in diet diversity (DDI) among the six regions (Table 1). Diet diversity was greatest in the eastern Aleutian Islands (DDI = 4.0) and least diverse in Area 3 of the central Aleutian Islands (DDI = 1.6).

During 1990–1994, the adult and juvenile Steller sea lion population in Alaska decreased by 20.7% (Strick et al. 1997). Populations of adult and juvenile sea lions in specific study areas decreased up to 48.5% (Table 1). Diet diversity was negatively correlated (Pearson $r = -0.994$, $P = 0.004$) with population trends in the six areas (Fig. 3). The less diverse the diet the more an area's population declined. We also compared the FO values for each category with population change; small schooling fish were the only category with a significant correlation (Pearson $r = 0.8144$, $P = 0.05$).

Temporal differences

Scats collected from Bogoslof and Ugamak islands in the eastern

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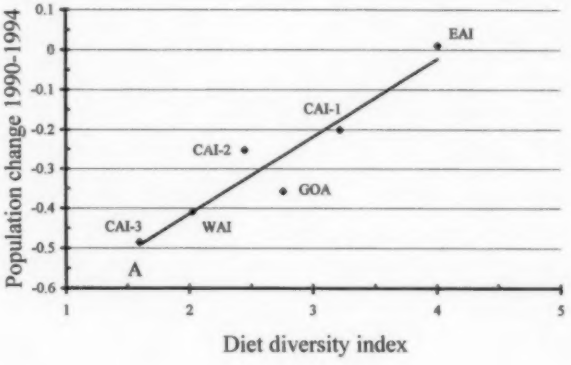
Aleutian Islands during the summers of 1985–1989 contained only three prey categories: gadids (n = 39, FO = 0.867), salmon, (n = 6, FO = 0.083), and cephalopods (n = 4, FO = 0.050). Gadid (mostly walleye pollock) consumption was less in 1990–1993 (FO = 0.372) than in 1985–1989 (χ^2 = 23.47, P < 0.001). There was no difference between years (1990–1993) in the proportion of sea lions consuming flatfish (FO = 0.0), salmon (FO = 0.061), or cephalopods (FO = 0.088). All other prey were consumed more frequently in the 1990–1993 period: small schooling fish (FO = 0.037, χ^2 = 9.89, P = 0.002), other demersal fish (FO = 0.079, χ^2 = 7.54, P = 0.006), and Atka mackerel (FO = 0.364, χ^2 = 26.61, P < 0.001). The diet diversity index for the 1985–1989 collection was 1.6, and the 1989 population was 54.0% of the 1985 population (point "A" on Fig. 3).

Gadids were the most common summertime prey in the Kodiak Island area in the 1985–1986 and 1990–1993 collections, but not in the 1976–1978 collection (Table 2). Of 54 scats from 1990 to 1993 with identifiable remains, 46 (85.2%) contained gadids compared with 32.1% of stomachs in collections from 1976 to 1978 (χ^2 = 23.49, P < 0.001) and 60.0% of stomachs in 1985–1986 (χ^2 = 5.46, P = 0.019). Salmon and small schooling fish were the second most common prey in the 1990–1993 collection (18.5% of scats each). Salmon consumption did not differ from the earlier collections. Small schooling fish consumption was not different from that recorded in 1985–1986, but was less than in 1976–1978 (60.7% of stomachs; χ^2 = 14.86, P < 0.001). At that time, small schooling fish (mostly capelin) were the most common prey in the summer Kodiak Island collections. The 1990–1993 collection included only one sample with capelin; the remainder were either Pacific sand lance (n = 4), Pacific herring (n = 4), or unidentifiable osmerids (n = 1). Flatfish were the fourth most common prey in 1990–1993 (13.0% of scats). This was greater than observed in either of the previous collections and was different (χ^2 = 3.97, P = 0.046) from 1976–1978 when no flatfish were found in the summer Kodiak Island area stomachs. The proportion of sea lions consuming cephalopods did not differ between periods. Atka mackerel and other demersal fish were not found in any of the Kodiak Island samples.

Discussion

The high correlation between area-specific diet diversity and population change supports the hypothesis that diet is linked with the Steller sea lion population decline in Alaska. Additional support for this linkage comes from the increase in diet diversity observed in the eastern Aleutian Islands area between 1985–1989 (a period of large decline) and 1990–1993 (a period of stability). The Kodiak Island data also support this hypothesis. Pitcher (1981) found that capelin and walleye pollock were common in the sea lion summer diet during the 1970s. Merrick and Calkins (1996) found that the 1985–1986 summer diet in the Kodiak Island area had increased its focus on walleye pollock (despite declines in juvenile walleye pollock abundance), and capelin was gone from the diet. They suggested that this may have contributed to the moderate population declines that occurred there between the 1970s and 1980s. The 1990–1993 diet indicated a further concentration of the diet on walleye pollock since the 1985–1986 period, and

Fig. 3. Steller sea lion DDI (based on scat analysis) compared with population declines experienced during 1990–1994 at rookeries in six areas. Point "A" is comparable data from the eastern Aleutian Islands collected during 1985–1989. The regression line was fit to the equation $y = 0.195x - 0.804$ ($r^2 = 0.901$, $P < 0.01$) for the six areas' 1990–1993 DDIs (x) and 1990–1994 rookery population changes (y).



the sea lion population has since gone through a severe decline (Strick et al. 1997).

The available data suggest that the Steller sea lion diet was different prior to the onset of the declines, which began in the eastern Aleutian Islands in the early 1970s and in the Gulf of Alaska in the early 1980s (Merrick et al. 1987). Fiscus and Baines (1966) found capelin in nine and Pacific sand lance in five of 14 sea lion stomachs collected in the eastern Aleutian Islands and Gulf of Alaska during 1960–1962. Walleye pollock and Atka mackerel were each found in one stomach. In a single summer's collection at Chernabura Island in 1960 (n = 74 stomachs with contents), 12 stomachs were found with "smelt" (perhaps capelin), 10 with "greenling" (perhaps Atka mackerel), seven with rockfish, five with sculpins, and 19 with cephalopods (Mathisen et al. 1962). No walleye pollock were found. Similarly, Pitcher (1981) found capelin in 61% of the stomachs of sea lions collected in the Kodiak Island area in the summers of 1975–1978. Subsequent studies, including this study, have failed to find capelin in significant numbers of stomachs. Of these predecline studies, only the 1975–1978 Kodiak Island collection included a substantial amount of walleye pollock (32% of stomachs).

No Steller sea lion food habits study has found a stable or increasing population maintained on a diet consisting mostly of either walleye pollock or Atka mackerel; it appears that at least two major prey need to be commonly available (e.g., walleye pollock and Atka mackerel in the eastern Aleutians in 1990–1993 and walleye pollock and capelin in the Kodiak area in 1975–1978). The eastern Aleutian Islands data further suggest that having secondary prey available stabilizes sea lion numbers. However, this apparent need for multiple prey is not necessarily due to differences in the energetic density of prey. Fadely et al. (1994) found that California sea lions (*Zalophus californianus*) maintained mass equally well on diets of either walleye pollock (4.6 kJ·g wet mass^{-1}) or herring (6.0 kJ·g wet mass^{-1}). This suggests that the advantage of using several prey is one of foraging efficiency. Diverse prey is easier to find

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Table 2. Proportion of Steller sea lion stomachs and scats containing seven prey categories for summer Kodiak Island area collections made during 1976–1978, 1985–1986, and 1990–1993.

Period	Sample size	Gadids (%)	Salmon (%)	Small schooling (%)	Flatfish (%)	Other demersal (%)	Atka mackerel (%)	Squid or octopus (%)
1990–1993	54	85.2	18.5	18.5	13.0	0.0	0.0	11.1
1985–1986	20	60.0	5.0	20.0	5.0	0.0	0.0	20.0
1976–1978	28	32.1	17.9	60.7	0.0	0.0	0.0	0.0

(more prey patches), capture (patch densities are increased), and handle (prey size is correct).

Source(s) of the diet differences

The 1990–1993 diets appear to reflect a combination of the sea lions' preference for relatively small (< 30 cm) schooling midwater fishes (Merrick and Calkins 1996) and changes in the diversity and abundance of prey species. In the Aleutian Islands region, Atka mackerel biomass increased significantly after the early 1980s (Lowe and Fritz 1994). Abundance of small walleye pollock on the eastern Bering Sea shelf was also high during 1989–1993 as a result of the strong 1989 year-class (Wespestad 1994). Thus, sea lions in the eastern Aleutian Islands may have benefitted from positive trends in prey abundance from both the Aleutian Islands and the eastern Bering Sea and had multiple abundant schooling prey available during 1990–1993.

Sea lions in most other areas generally consumed only one category of schooling prey, probably because of the low abundance of such prey. Walleye pollock abundance decreased through most of the central and western Aleutian Islands during the 1980s and 1990s while Atka mackerel populations were increasing (Lowe and Fritz 1994; Wespestad 1994). This restricted sea lions there to a diet composed largely of Atka mackerel. In the Gulf of Alaska, Atka mackerel biomass has remained very low since the early 1980s (1993 adult biomass = 21 600 t (metric tons); Lowe and Fritz 1994). Walleye pollock biomass was reduced and declining through 1993, but walleye pollock biomass remained much greater than that of Atka mackerel (1993 adult biomass = 1 062 000 t; Hollowed et al. 1994). However, most of the walleye pollock biomass in 1990–1993 consisted of large, older fish from the 1984–1985 year-classes. These fish were larger than those that sea lions normally consume (Merrick and Calkins 1996).

The other feature distinguishing the diet of eastern Aleutian Islands sea lions from other areas was the common consumption of other categories of prey. Salmon and small schooling fish constituted more than 10% of the diet. Salmon abundance was high in Alaska during 1990–1993 (Hare and Francis 1995) and they were relatively common in sea lion diets from almost all areas. However, the eastern Aleutian Islands area was the only area where small schooling fish (Pacific herring and Pacific sand lance) and other demersal fish made up a significant part of the diet. This suggests that these prey are more common in the area, but there is little research to document this. Prey surveys begun in 1994 by NMFS, USF&WS, and University of Alaska in the eastern Aleutian Islands to central Gulf of Alaska area suggest that pelagic and demersal fish abundance is highest in the eastern Aleutian Islands (NMFS, 7600 Sand Point Way, Seattle, Wash., unpublished data; B. Norcross, University of Alaska, Fairbanks, Alaska, personal communication). If availability of small schooling and demersal fish prey has increased in the eastern Aleutian Islands, it may be a result of recent declines in the abundance of piscivorous, adult walleye pollock (Wespestad 1994; Merrick 1996). Conversely, the recent record high abundance of piscivorous, adult arrowtooth flounder in the Gulf of Alaska could be partly responsible for the apparent low abundance of small fish prey there (Wilderbuer and Brown 1992; Merrick 1995).

In conclusion, it should be recognized that these results reflect only the diets of successfully foraging adult females in summer. Sea lions who do not find prey leave no record of their failure in scat analyses. However, we believe that these analyses still represent a reasonable index of the prey field sampled by foraging sea lions. This is because the collections integrate across a range of foraging successes, including sea lions who forage poorly but find some prey as well as those sea lions who forage quite well and maintain a rich diet. Still, the apparent relationship found between summer diets and the pattern of decline was unexpected because food limitation has been predicted to most heavily affect juvenile sea lions in winter (Loughlin and Merrick 1989). Juvenile sea lions appear to be less adept foragers than adults (Merrick et al. 1994; Merrick 1995) and juveniles have a more restricted diet than adults (Merrick and Calkins 1996). Prey densities are also lower in winter near sea lion haul-outs; many prey (e.g., Atka mackerel, salmon, capelin, and herring) are only found nearshore in summer during spawning, and in winter are only available offshore and in deeper water. Thus, any indication of scarcity seen in the summer adult diet could be magnified in winter, particularly for juvenile sea lions. Our results suggest that summer diets of adult females index the prey available to juvenile sea lions in winter. Perhaps this is due to the absence or presence of the small fish in both diets because the large size of adult walleye pollock and Atka mackerel may make these prey difficult for small sea lions to capture and consume. Insofar as juvenile survival is related to their foraging success, then increased diversity in the adult diet would correlate well with improved population trends.

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Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River

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Abstract: We related the arrival timing of adult sockeye salmon (*Oncorhynchus nerka*) at a series of dams on the Columbia River (Bonneville, McNary, and Rock Island) and Snake River (Ice Harbor) to the changing flow and temperature regimes over the last several decades. The temperatures experienced by sockeye salmon have increased in the lower but not upper reaches of the system, and the flows experienced by the fish have decreased. The Bonneville–McNary travel rate increased from about 22 to 49 km/day, and sockeye salmon now pass McNary Dam about 11 days earlier than in 1954. Both travel rate and arrival date were correlated with temperature increases and flow decreases at McNary during that period. Sockeye salmon arrival at Rock Island Dam (14 days earlier from 1933 to 1994) was also correlated with temperature and flow there. However, the travel rate between McNary and Rock Island dams did not change from 1955 to 1994, despite a decrease in estimated water velocity from 85 to 23 km/day. Sockeye salmon arrival at Ice Harbor Dam has sometimes been bimodal; the first mode's date has not changed, but annual mean dates have been positively correlated with flow and negatively with temperature.

Résumé : Nous avons relié le moment d'arrivée de saumons sockeye (*Oncorhynchus nerka*) adultes à une série de barrages situés sur le fleuve Columbia (Bonneville, McNary et Rock Island) et la rivière Snake (Ice Harbor) aux régimes d'écoulement et de température qui ont changé au cours des dernières décennies. Les températures ont augmenté dans les segments inférieurs, mais non dans les segments supérieurs du système, et les débits ont diminué. La vitesse de migration entre les barrages de Bonneville et McNary a augmenté, passant de 22 à 49 km/jour, et le saumon sockeye franchit maintenant le barrage de McNary environ 11 jours plus tôt qu'en 1954. La vitesse de migration et la date d'arrivée ont toutes deux été corrélées avec les augmentations de la température et les diminutions de débit au barrage de McNary durant cette période. L'arrivée du saumon sockeye au barrage de Rock Island (14 jours plus tôt en 1994 qu'en 1933) était également corrélée avec la température et le débit à cet endroit. Cependant, la vitesse de migration entre les barrages McNary et Rock Island n'a pas changé entre 1955 et 1994 en dépit d'une diminution de la vitesse estimée de l'eau de 85 à 23 km/jour. L'arrivée du saumon sockeye au barrage d'Ice Harbor a parfois été bimodale; la date du premier mode n'a pas changé, mais les dates annuelles moyennes ont été corrélées positivement avec l'écoulement et négativement avec la température.
[Traduit par la Rédaction]

Introduction

The migratory timing of adult salmon is hypothesized to be an adaptation to the long-term average regimes of temperature, flow, and other physical factors experienced by adults returning from the ocean that might affect prespawning mortality (Gilhousen 1990), the distance that the fish must migrate to their spawning grounds, and the optimal spawning date. Migratory timing is under partial genetic control (e.g., Atlantic salmon (*Salmo salar*), Hansen and Jonsson 1991; pink salmon (*Oncorhynchus gorbuscha*), Gharrett and Smoker 1993). The date of sexual maturation or spawning is also under genetic control (e.g., rainbow trout (*Oncorhynchus mykiss*), Siitonen and Gall 1989). The spawning date is affected by the need to maximize survival of embryos (affected by such factors as temperature and flow regimes) and the survival and growth opportunities for newly emerged fry (Brannon 1987; Brännäs 1995).

Although there is considerable genetic control over the timing of upstream migration and spawning, environmental factors also play an important role; ocean temperature has been correlated with the arrival of sockeye salmon (*Oncorhynchus nerka*) in coastal waters (Burgner 1980; Blackbourn 1987; Quinn 1990). In addition to possible oceanic influences on arrival in coastal waters, river temperature and flow can affect upstream migratory behavior and timing (reviewed by Banks 1969; Jonsson 1991; Trépanier et al. 1996). In some streams, water levels may be insufficient for entry (e.g., coho salmon (*Oncorhynchus kisutch*), Shapovalov and Taft 1954) and increasing flows may stimulate upstream migration when water levels are low (Atlantic salmon, Smith et al. 1994), but the relationships of flow and temperature to migration are not consistent (Trépanier et al. 1996). Large rivers have sufficient water for entry at all times of the year, but discharge and temperature may nevertheless affect upstream migration. The Columbia River's flow and temperature have been correlated with the arrival of American shad (*Alosa sapidissima*) (Leggett and Whitney 1972) and sockeye salmon (Quinn and Adams

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Fig. 1. Map of the Columbia River system showing major dams: BN, Bonneville; DA, The Dalles; JD, John Day; MN, McNary; PR, Priest Rapids; WA, Wanapum; RI, Rock Island; RR, Rocky Reach; WE, Wells; CJ, Chief Joseph; GC, Grand Coulee; KE, Keenleyside; MI, Mica; DU, Duncan; LI, Libby; IH, Ice Harbor; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite; HC, Hells Canyon.

1996) at Bonneville Dam. The influence of these environmental factors is particularly interesting because management of the river for hydroelectric power production has led to decreasing discharges and warming of the lower river in late spring and early summer over the last five decades (Quinn and Adams 1996). The river's warming (e.g., first date of 15.5°C water) occurs about 30 days earlier now than in the past (i.e., 1938–1993), the annual maximum temperatures have increased by about 1.8°C from 1949 to 1993, and fall cooling of the river has been occurring later in the season (Quinn and Adams 1996). The increasing temperatures and decreasing flows were both correlated with progressively earlier arrivals of sockeye salmon at Bonneville Dam (about 6 days from 1949 to 1993).

Maturing sockeye salmon arrive at Bonneville Dam (river km (rkm) 234, Fig. 1) in early summer (primarily June and July) and the trends in temperature, flow, and earlier arrival of salmon there pose questions regarding trends in environmental conditions and salmon travel rates farther upriver. Many sockeye salmon populations in the Columbia River system were eliminated prior to the construction of Bonneville Dam (Mullan 1986; Fryer 1995), and currently the great majority spawn in tributaries of lakes Wenatchee and Osoyoos in September and October (Mullan 1986). These sites are 842 and 986 km

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from the mouth of the Columbia River, respectively (Poe and Mathisen 1981). Populations with even more arduous migrations to the lakes in the Sawtooth Mountains of Idaho (Bjornn et al. 1968)(approximately 1600 km) have been increasingly scarce during the past decades (Chapman et al. 1990; Fryer 1995). Long or difficult migrations may select for efficient energy use per unit distance traveled (Bernatchez and Dodson 1987), as migrations can deplete the energy resources of salmon (Gilhousen 1980). Populations with arduous migrations show lower levels of reproductive output (ovary weight) than populations with shorter migrations (Linley 1993). Prespawning mortalities of Fraser River sockeye salmon were highest for upriver populations migrating in the summer and were positively correlated with river temperatures for most populations (Gilhousen 1990). To the extent that the energetically demanding migrations of Columbia River sockeye salmon have become more stressful, because of warmer temperatures, or less challenging, because of reduced flows, the survival and fitness of salmon may be affected.

The aim of this study was to quantify the changes in flow and temperature that have occurred in the Columbia River during the period of extensive development for hydroelectric production and understand how these factors have affected the migratory patterns of adult sockeye salmon. We selected sockeye because, unlike other salmonids (e.g., coho salmon, chinook salmon *(Oncorhynchus tshawytscha)* and steelhead (*O. mykiss*)), they are essentially all wild, native, and are produced in a few systems with relatively similar timing (see Mullan 1986 and Fryer 1995 for details of their history and status). Thus the variation in relative abundance of populations with different timing or effects of hatchery propagation that would confound studies on the other species are much less significant problems for the analysis of sockeye salmon migration. We compared trends in temperature and flow at Bonneville Dam (the lowermost dam on the Columbia River) with data from McNary Dam (rkm 470), representing the river below its confluence with the Snake River, Priest Rapids (rkm 639) and Ice Harbor (rkm 537) dams, representing the lowermost dams on the Columbia and Snake rivers above their confluence, respectively, and Rock Island Dam (rkm 725), representing the uppermost dam passed by both the Lake Wenatchee and Lake Osoyoos sockeye salmon runs. We determined the salmon arrival patterns (median date and temporal distribution) at these dams over the periods of record and tested the null hypothesis that travel rate (relative to land) has remained constant over time. If so, the changing passage dates at Bonneville Dam (Quinn and Adams 1996) would be reflected at dams farther upstream. This was contrasted with the alternative hypotheses that travel rate has decreased or increased over time.

Methods

Sources of data

The U.S. Army Corps of Engineers annual fish passage reports (1938–1994) were the source of data on temperature, flow, and abundance and timing of sockeye salmon passing Bonneville, McNary, and Ice Harbor dams. Unpublished data for Priest Rapids Dam were acquired from the Center for Quantitative Science, University of Washington, and did not include sockeye salmon counts. At Bonneville Dam, sockeye salmon were counted by direct observation from windows at the Bradford Island and Washington shore fish ladders. The fish ladders serve as the primary routes of passage for migrating fish, although some fish use the dam's navigation lock while vessels are transiting. From April 1 to October 31 (encompassing the sockeye salmon spawning migrations), fish were counted from 04:00 to 20:00 PST. During counting hours, personnel observed for 50 min of each hour. Simple expansion provided an estimate of the number of fish passing each hour. Nighttime video monitoring in 1992 and 1993 showed that fewer than 10% of the sockeye salmon passed through the ladder during the 8 h normally omitted from the counts. For consistency, we did not add night counts from 1992 and 1993 to daytime counts.

McNary Dam sockeye salmon counts were performed in the Washington and Oregon fish ladders between April 1 and October 31, usually from 04:00 to 20:00 PST. There was some slight variation in the counting hours from year to year. In most years, fish were counted by direct observation, but in some years (1975–1986), this was combined with closed-circuit color television. Some years (1957–1966) included periods of "sample counting" in which counts were performed for 4-h periods, alternating between the two ladders, for 16 h daily. The data set accounted for these different counting hours, and for breaks taken by personnel during regular counting hours, by simple expansion. Any sockeye counted before April 1 or after October 31 were omitted for consistency among years, but data from years with counts in March, November, and part of December showed that fewer than 0.005% of the total annual run passed during these months.

The data from McNary Dam in 1972 and 1974 combined night counts (from 20:00 to 04:00 PST) with counts during the normal daytime hours for approximately half the dates. Studies at other dams indicated that far fewer sockeye salmon ascended at night than during the day. Night to day ratios were 0.05 at Bonneville Dam, 0.07 and 0.14 at the south and north counting stations at The Dalles Dam, and 0.09 at John Day Dam (Calvin 1975). No such studies were done for sockeye salmon at McNary Dam, but we estimated the daily counts for dates that included nighttime counts by dividing the total daily count by 1 + 0.08 (average correction factor from the other dams).

We wished to analyze salmon passage with respect to average daily temperature at each of the dams. However, daily water temperatures at McNary Dam were reported as maxima and minima for 1954–1959, as maxima from 1960 to 1961, and as average from 1962 to the present. We estimated the daily average temperature as the mean of the maximum and minimum daily values for 1954–1959. For 1960–1961, when only maxima were available, we used the average difference of 0.20°C between maximum and average daily value (1954–1959 data) to adjust the 1960–1961 values to approximate daily averages. The location where the McNary Dam water temperatures were taken changed during the 1970s. Before the 1970s, the location was not documented but was apparently in the fish ladders. Since the mid-1970s, temperatures have been taken at the scroll case of the turbine. Compared with the previous method, the temperatures taken at the turbine should be cooler and show less diurnal fluctuation because the water is drawn deeper than the water supplying the fish ladder (J. McKern, U.S. Army Corps of Engineers, personal communication).

The temperature data for Priest Rapids Dam contained some obvious outliers that were assumed to be errors in recording or transcription. Temperatures for these days were interpolated from the surrounding dates. At Ice Harbor Dam, sockeye salmon were counted by direct observation and closed-circuit television (1976–1994) in the north and south fish ladders. All years had counts from April 1 to October 31, from 04:00 to 20:00 PST. There was counting before April in some years, but no sockeye were recorded. In nine years that included counts after October 31, only one year had any sockeye recorded in November or December, and they amounted to only 1% of the annual total run. Some days in 1972 and 1974 included night counts, and they were adjusted in the same way as the McNary Dam counts.

Sockeye abundance and timing data, as well as temperature and

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flow data, for Rock Island Dam from 1933 to 1994 were provided by Chelan County Public Utility District. Some years had no sockeye data (1939, 1953, 1954, 1963, 1968–1972) or no flow data (1940, 1953, 1973, 1986). The counting dates varied substantially among years but included at least from early May to late September for all years except 1933 and 1934. Most years had daily counts, but several years (1934, 1940–1943) had only weekly counts that we assigned to the middle day of the week.

Data analysis

To evaluate temperature and flow trends, we selected the following variables for each year at McNary (1954–1994), Ice Harbor (1962–1994), Priest Rapids (1975–1994), and Rock Island (1933–1994) dams: mean flow and temperature for June 1 – July 31, annual maximum temperature, the date of maximum temperature, and the first and last days of the year with a temperature ≥15.5°C. The 15.5°C (60°F) temperature was an arbitrary measure used to study variation in the dates of spring warming and fall cooling, chosen for consistency with previous studies (Leggett and Whitney 1972; Quinn and Adams 1996). Temperatures were recorded in Fahrenheit and converted to Celsius. Flow data were recorded in cubic feet per second and were converted to cubic metres per second. We analyzed temperature and flow over the June–July period because these months encompassed 96, 87, and 84% of the annual total runs at McNary, Ice Harbor, and Rock Island dams, respectively. Unless otherwise stated, "flow" and "temperature" refer to June–July means. If the maximum temperature occurred on several days rather than just one, the middle date was used. Simple linear regressions were performed with each of the above variables to test for changes in these environmental conditions over time at each of the dams.

We performed simple linear regressions between water temperature and flow means at the dams to better understand the relationship between these two variables. For each of McNary, Ice Harbor, Priest Rapids, and Rock Island dams, the June–July temperature was regressed against June–July flow. However, temperature and flow could show concurrent trends over time (i.e., be statistically correlated) yet be unconnected. Residual analyses were used to test for underlying relationships between temperature and flow at each of the dams. For each year, the residual (difference between the observed value and that predicted by the overall trend) was calculated for mean temperature and flow. The temperature residuals were then regressed against the flow residuals. To better understand long-term changes in temperature and flow in the lower Columbia, we estimated the relative proportions of Columbia and Snake River water combining at their confluence from the ratio of flows (June 1 – July 31) at Priest Rapids and Ice Harbor dams.

Peak sockeye salmon run dates were approximated by the day on which 50% of the annual run had passed the dam because the yearly frequency distributions of sockeye passage were approximately normal, with little kurtosis or bimodality except at Ice Harbor Dam (see below). Simple linear regressions of peak run date versus year were performed to test for changes in run timing at McNary and Rock Island dams. The dates of 5 and 95% sockeye passage were also calculated for each dam, as a measure of overall timing of the run. Counts at Ice Harbor Dam have been low in recent years (1985–1993 mean annual total = 16) and visual inspection revealed bimodal or highly skewed distributions in many years. There was virtually always a mode in July and in some years a second, smaller mode in September, separated by periods of 3–6 weeks with few or no salmon counted. August 19 was the date that best characterized the end of the "early" mode of migration. To calculate migratory timing for comparison with the other dams, we calculated the 50% date for the early mode. We only used the 1962–1984 data because counts since 1985 have been too low for meaningful analyses. We regressed peak run dates for McNary, Ice Harbor (early mode), and Rock Island dams against temperatures and flows and then regressed the residuals of the peak run dates against the temperature and flow residuals.

To estimate the temperatures experienced by migrating sockeye, we calculated the weighted-mean migration temperature, T_W (Quinn and Adams 1996):

$$T_W = \sum n \cdot t / N$$

where n is the daily number of fish counted, N is the annual total number of fish, and t is the daily temperature.

The T_W thus weights observed temperatures by the number of fish migrating on days when that temperature was recorded. We used simple linear regressions to test for changes in T_W of sockeye at McNary, Ice Harbor (1962–1984), and Rock Island dams. To provide further insight into the more complex patterns observed at Ice Harbor Dam, we constructed a histogram of daily average temperatures, based on their frequency of occurrence from June 14 and October 26 (the first and last dates, respectively, when sockeye salmon were observed at the dam). We contrasted this envelope of available temperatures with the subset used by the salmon, calculated by weighting each temperature by the number of salmon passing the dam on days when the temperature was recorded.

We used the number of days between the 50% passage dates at Bonneville and McNary dams to estimate travel time between the dams and then converted it to travel rate (kilometres per day). Linear regression was performed to test for a change in the travel rates over the years and to analyze travel rates with respect to temperature and flow at McNary Dam. This was followed by regression of travel rate residuals against temperature and flow residuals to test for underlying relationships.

In studying sockeye timing between Bonneville and McNary dams, we were concerned that changes in sockeye disorientation, caused by dams constructed during the period of study, might have affected trends in travel rate. The two dams between Bonneville and McNary dams, The Dalles Dam (rkm 306) and John Day Dam (rkm 347), were both operating by 1968, so the 1968–1994 time period provided an opportunity to examine the possible influences of flow and temperature changes on sockeye salmon migration without the confounding influence of new dams. Regression analysis on travel times and residual analyses of travel rate versus McNary mean flow and temperature over this period were performed.

We estimated the sockeye travel rates between McNary and Rock Island dams (1955–1994) and regressed these travel rates against the mean temperature and flow at Rock Island Dam and corresponding residuals. Travel times between McNary and Ice Harbor dams (using the early mode) were also analyzed, but the difference between 50% passage dates proved unreliable. Travel time estimates were negative in 8 of the 23 years from 1962 to 1984 and 7 of 23 were still negative if the whole Ice Harbor run was used instead of just the early mode. Snake River sockeye, which make up a relatively small portion of those passing McNary Dam, apparently migrate earlier than the other sockeye populations.

Finally, to better understand the changes in the river experienced by the salmon, we converted the flow data to water velocities, using equations from the Columbia River Salmon Project model (CRiSP 1) developed at the Center for Quantitative Science at the University of Washington. For each river segment for which we had fish travel rate data, we used the flows at each dam within the segment and weighted the velocities by the length of the reach between each dam to obtain an average water velocity for the whole segment.

Results

Water temperature and flow patterns

The river has been warming to 15.5°C significantly earlier at McNary Dam than in past years (15-day difference between 1954 and 1994, Table 1). The date of the annual maximum temperature has not changed but the mean June–July temperature

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Table 1. Linear regression results for river conditions at McNary, Ice Harbor, Priest Rapids, and Rock Island dams.

Relationship	Dam	Years	r^2	Slope	Intercept	p
1st 15.5° vs. year	MCN	1954–1994	0.16	–0.39	June 27	0.011
Last 15.5° vs. year	MCN	1954–1994	0.27	0.29	Oct. 12	<0.001
T_{MAX} vs. year	MCN	1954–1994	0.13	0.03	20.8°	0.022
T_{MAX} date vs. year	MCN	1954–1994	0.01	–0.09	Aug. 19	0.506
Temp vs. year	MCN	1954–1994	0.19	0.04	15.9°	0.005
Flow vs. year	MCN	1954–1994	0.56	–184.7	11 641	<0.001
Temp vs. flow	MCN	1954–1994	0.56	–0.0003	N/A	<0.001
$Temp_{RES}$ vs. $Flow_{RES}$	MCN	1954–1994	0.50	–0.0003	N/A	<0.001
1st 15.5° vs. year	IHR	1962–1994	0.01	–0.08	June 21	0.686
Last 15.5° vs. year	IHR	1962–1994	0.28	0.34	Oct. 13	0.001
T_{MAX} vs. year	IHR	1962–1994	0.33	–0.06	23.7°	<0.001
T_{MAX} date vs. year	IHR	1962–1994	0.04	0.27	Aug. 13	0.236
Temp vs. year	IHR	1962–1994	0.0003	–0.002	17.0°	0.926
Flow vs. year	IHR	1962–1994	0.14	–35.97	2646	0.030
Temp vs. flow	IHR	1962–1994	0.57	–0.0010	N/A	<0.001
$Temp_{RES}$ vs. $flow_{RES}$	IHR	1962–1994	0.68	–0.0011	N/A	<0.001
1st 15.5° vs. year	PRD	1975–1994	0.16	–0.94	July 4	0.084
T_{MAX} vs. year	PRD	1975–1994	0.26	0.16	18.7°	0.022
T_{MAX} date vs. year	PRD	1975–1994	0.002	–0.11	Aug. 23	0.868
Temp vs. year	PRD	1975–1994	0.16	0.07	14.9°	0.078
Flow vs. year	PRD	1975–1994	0.006	–14.6	3979	0.744
Temp vs. flow	PRD	1975–1994	0.43	–0.0006	N/A	0.001
$Temp_{RES}$ vs. $flow_{RES}$	PRD	1975–1994	0.47	–0.0006	N/A	<0.001
PRD:IHR flow vs. year	PRD	1975–1994	0.24	0.09	1.6	0.029
1st 15.5° vs. year	RID	1933–1994	0.006	–0.47	July 9	0.547
Last 15.5° vs. year	RID	1933–1994	0.22	0.27	Oct. 8	<0.001
T_{MAX} vs. year	RID	1933–1994	0.01	0.007	18.9°	0.391
T_{MAX} date vs. year	RID	1933–1994	0.03	0.13	Aug. 21	0.179
Temp. vs. year	RID	1933–1994	0.01	0.005	14.4°	0.439
Flow vs. year	RID	1933–1994[a]	0.42	–92.1	9316	<0.001
Temp vs. flow	RID	1933–1994[a]	0.39	–0.0002	N/A	<0.001
$Temp_{RES}$ vs. $flow_{RES}$	RID	1933–1994[a]	0.50	–0.0003	N/A	<0.001

Note: Variables: the first and last date on which the recorded water temperature was 15.5°C (1st 15.5°, last 15.5°), the maximum temperature recorded (T_{MAX}), the date of the annual maximum temperature (T_{MAX} date), the mean daily temperature (°C) and discharge (m^3/s) for June 1 – July 31 (temp, flow), the period of record (year), and the ratio between Priest Rapids Dam and Ice Harbor Dam June–July flows (PRD:IHR flow). Residuals of the above variables were denoted by subscript RES. All intercepts for regressions involving years are for the first year in the data period.

[a]Years with missing data.

(Fig. 2) and maximum temperature increased by 1.5 and 1.2°C, respectively, since 1954, and fall cooling of the river below 15.5°C at McNary Dam has been occurring 12 days later. The mean flow decreased by more than 50% from 1954 to 1994 (Fig. 3) and the estimated water velocity for the Bonneville Dam – McNary Dam segment decreased from 69 to 25 km/day. The strong correlations between June–July temperature and flow, and their residuals, indicated a link between declining flow and water temperature increases (Table 1).

At Priest Rapids Dam on the Columbia River above the confluence with the Snake River, the mean temperature and dates of maximum temperature, first 15.5°C, and last 15.5°C have not changed significantly since 1975 (Table 1). The maximum temperature, however, has increased by about 3°C from 1975 to 1994. The mean flow at Priest Rapids Dam did not change significantly between 1975 and 1994, but the ratio of Priest Rapids Dam to Ice Harbor Dam flows increased from 1975 to 1994, resulting from the reduction in Snake River flow (Table 1).

Regressions showed no significant changes in either the first 15.5°C date or the date of maximum temperature at Rock Island Dam (Table 1). The fall cooling of the river below 15.5°C became significantly later between 1933 and 1994, amounting to a difference of 17 days. Trends in the annual maximum temperature and the mean summer temperature at the dam were similar to each other, decreasing until the late 1960s and increasing thereafter (Fig. 2). The average flow at Rock Island Dam before 1974 was approximately halved after 1974 (Fig. 3). The mean water velocity for the McNary Dam – Rock Island Dam segment decreased from 85 to 23 km/day over the 1955–1994 period.

The dates of first 15.5°C and maximum temperature of the Snake River at Ice Harbor Dam have not changed significantly, but fall cooling became 11 days later from 1962 to 1994 (Table 1). Over the same period the mean temperature did not change (Fig. 2), but the maximum temperature decreased by about 1.9°C, and the flow decreased significantly

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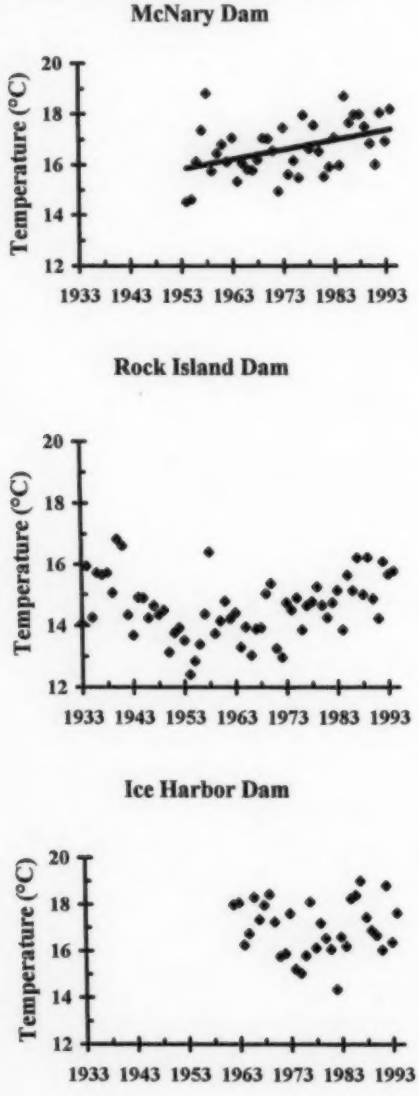
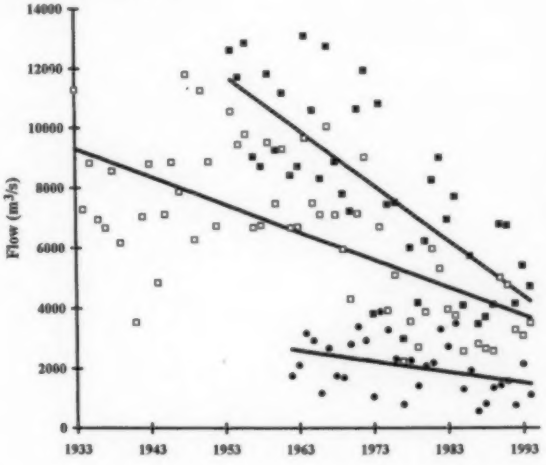
Fig. 2. Trends in June–July mean temperatures of the Columbia River at McNary (1954–1994) and Rock Island (1933–1994) dams and the Snake River at Ice Harbor Dam (1962–1994).



(Fig. 3). June–July temperature and flow, and their residuals, were highly correlated (Table 1).

Fig. 3. Trends in mean June–July flows of the Columbia River at McNary (solid squares, 1954–1994) and Rock Island (open squares, 1933–1994) dams and the Snake River at Ice Harbor Dam (solid circles, 1962–1994).



Sockeye salmon migratory timing

Sockeye salmon have been passing McNary Dam progressively earlier from 1954 to 1994, amounting to a difference of about 11 days (Table 2). The peak date was correlated negatively with temperature and positively with flow at McNary Dam. Residuals of the 50% date were normally distributed and were correlated with residuals of temperature and flow. Regression analysis of the T_W showed no significant change (Table 2). As at McNary Dam, the peak run date at Rock Island Dam became progressively earlier, amounting to a difference of 14 days from 1933 to 1994 (Table 2). Dates of 50% passage were correlated with both temperature and flow, and their residuals, at Rock Island. There was a significant decrease of about 2°C in T_W between 1933 and 1994.

The overall arrival pattern at Ice Harbor Dam was bimodal (Fig. 4), but in some years, only the early mode was observed. The 50% date of the first mode of sockeye salmon at Ice Harbor Dam did not change from 1962 to 1984, but migratory timing was positively correlated with flow and negatively correlated with temperature (Table 2). There was a significant decrease in T_W from 1962 to 1984. That is, on average, sockeye salmon experienced cooler temperatures in that section of the system in the 1980s than they did previously. Between 1985 and 1993 the T_W had been higher, but the salmon had been so scarce (mean annual total = 16) that these T_W values are unreliable and not comparable with those of the previous years. Histograms (Fig. 5) of temperatures at which sockeye passed the dam and temperatures available during the passage period showed that few sockeye passed at the lower temperatures that occurred at the beginning and end of the passage period. Most sockeye passed at temperatures around 20.0°C, and few sockeye passed at temperatures above 22.2°C, although these temperatures often occurred.

Travel rates between dams

The Bonneville–McNary travel rate between 1954 and 1994 increased from 21.6 to 48.6 km/day (Fig. 6), equivalent to a travel time change from 10 to 5 days (Table 3). There was a negative correlation between travel rate and mean flow at McNary Dam; as flow decreased, travel rate increased. Residuals of travel rate and flow were normally distributed and correlated with travel rate, indicating that years with especially low flow compared with that expected from the overall trend also had faster travel rates than expected. Warmer water at McNary Dam was also associated with faster travel rates and the residuals of travel rate were positively correlated with the temperature residuals.

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Table 2. Linear regression results for adult sockeye passage at McNary, Ice Harbor, and Rock Island dams.

Relationship	Dam	Years	r^2	Slope	Intercept	p
50% date vs. year	MCN	1954–1994	0.49	–0.28	July 14	<0.001
T_W vs. year	MCN	1954–1994	0.05	0.02	17.3°	0.153
50% date vs. temp	MCN	1954–1994	0.44	–3.01	N/A	<0.001
50% $date_{RES}$ vs. $temp_{RES}$	MCN	1954–1994	0.32	–2.01	N/A	<0.001
50% date vs. flow	MCN	1954–1994	0.66	0.0013	N/A	<0.001
50% $date_{RES}$ vs. $flow_{RES}$	MCN	1954–1994	0.36	0.0011	N/A	<0.001
50% date vs. year	IHR	1962–1984	7×10^{-5}	–0.008	July 10	0.969
T_W vs. year	IHR	1962–1984	0.35	–0.10	19.6°	0.003
50% date vs. temp	IHR	1962–1984	0.19	–2.39	N/A	0.037
50% $date_{RES}$ vs. $temp_{RES}$	IHR	1962–1984	0.27	–3.28	N/A	0.012
50% date vs. flow	IHR	1962–1984	0.38	0.0045	N/A	0.002
50% $date_{RES}$ vs. $flow_{RES}$	IHR	1962–1984	0.39	0.0046	N/A	0.001
50% date vs. year	RID	1933–1994[a]	0.43	–0.23	July 26	<0.001
T_W vs. year	RID	1933–1994[a]	0.36	–0.03	17.6°	<0.001
50% date vs. temp	RID	1933–1994[a]	0.27	–3.70	N/A	<0.001
50% $date_{RES}$ vs. $temp_{RES}$	RID	1933–1994[a]	0.35	–3.2	N/A	<0.001
50% date vs. flow	RID	1933–1994[a]	0.63	0.0021	N/A	<0.001
50% $date_{RES}$ vs. $flow_{RES}$	RID	1933–1992[a]	0.39	0.0017	N/A	<0.001

Note: Variables: the date of 50% sockeye passage by a dam (50% date), the weighted-mean migration temperature (T_W), the mean daily temperature (°C) and discharge (m^3/s) for June 1 – July 31 (temp, flow), and the period of record (year). Residuals of the above variables were denoted by subscript RES.

[a]Years with missing data.

Fig. 4. Frequency distribution of sockeye salmon arrival dates at Ice Harbor Dam from 1962–1994 illustrating the bimodal pattern observed in many years.

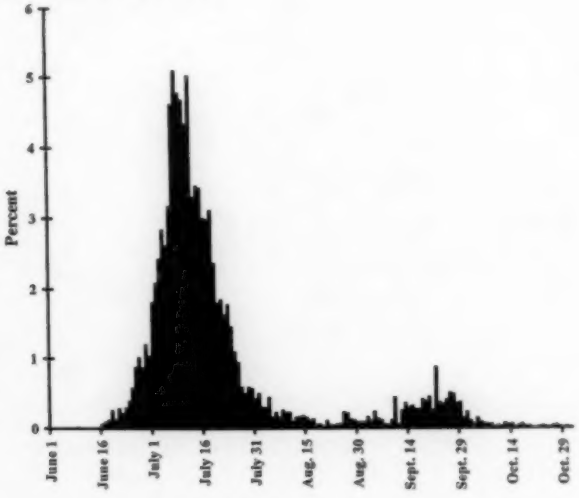
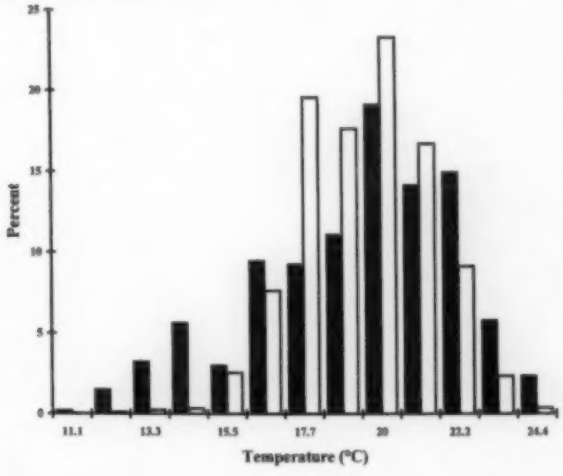


Fig. 5. Percent frequency of daily mean temperatures (black bars) at Ice Harbor Dam over the period of the summer when adult sockeye salmon have been observed passing the dam (June 14 – October 26) and percent frequency of temperatures (white bars), weighted by the number of sockeye salmon passing the dam on that day. Both data sets are from 1962 to 1984. Temperatures were converted from Fahrenheit.



From 1968 to 1994, when no new dams were constructed between Bonneville and McNary, the travel rate increased from 27.2 to 60.0 km/day (equivalent to a decrease in travel time of about 3.7 days) and was correlated negatively with flow and positively with temperature at McNary (Table 3). The residuals of travel rate were correlated with temperature residuals ($p = 0.024$) and weakly related to flow residuals ($p = 0.051$). The travel rate between McNary and Rock Island dams did not change from 1955 to 1994, averaging 29.8 km/day (Table 3), or 9 days travel time. Residuals of travel rate were weakly correlated with the residuals of flow at Rock Island Dam ($p = 0.057$) but not with temperature residuals ($p = 0.146$).

Discussion

Flows at Rock Island Dam increased from 1933 until the early 1950s, and Bonneville, McNary, and Rock Island dams all experienced a substantial decrease in flow since the 1950s.

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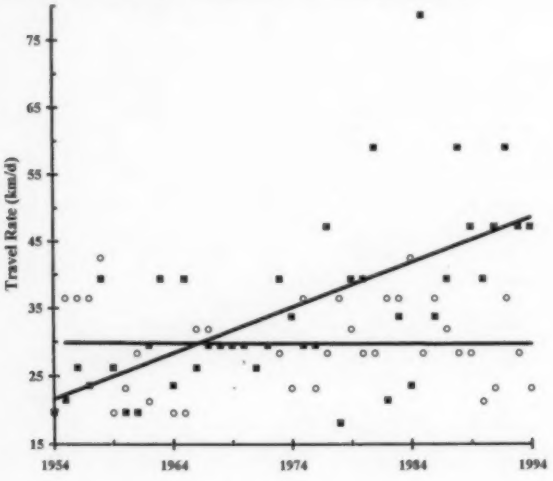
Fig. 6. Travel rate (ground speed) of adult sockeye salmon migrating between Bonneville and McNary dams (solid squares) and between McNary and Rock Island dams (open circles).



This decrease resulted from flow manipulation made possible by the great increase in storage capacity (e.g., the completion of Duncan (1967), Keenleyside (1968), and Mica (1973) dams in Canada and Libby Dam (1975) in the United States). Temperature trends similar to those described for Bonneville Dam (Quinn and Adams 1996) were evident at McNary Dam; spring warming has become earlier, June and July temperatures have become higher, and fall cooling has become later. The correlation between temperature trends at these two dams results from the relatively rapid travel times of water (approximately 5 days) through this reach of the Columbia River and the absence of major tributaries between dams. Some warming has occurred at Priest Rapids Dam on the mid-Columbia River, but peak temperatures have decreased at Ice Harbor Dam on the Snake River. Rock Island Dam records, earlier than those of the other dams, indicated decreasing temperatures until the 1960s. This is consistent with the general view that storage decreased peak temperatures (Jaske and Goebel 1967; Ebel et al. 1989), but temperatures have been increasing since then. It is unclear whether the recent warming trend is solely a consequence of flow management in the system or if climate change (Lettenmaier et al. 1994) plays a role.

The trends in sockeye passage between Bonneville and McNary dams supported our second hypothesis; travel rate relative to land increased from about 22 to 49 km/day from 1954 to 1994. Temperature, flow, and their residuals were correlated with travel rate, but the strong correlation between diminished flow and increased river temperatures made it impossible to separate their effects on sockeye salmon arrival dates and travel rates. The observed travel rates are within the range reported in other studies of salmon (Brett 1995) but much faster than those of sockeye salmon in areas of difficult passage in the canyon of the Fraser River (Hinch et al. 1996).

In contrast with the pattern observed for sockeye timing between Bonneville and McNary dams, the pattern observed over the same time period between McNary and Rock Island dams supported the null hypothesis. Sockeye salmon passage dates at both dams became earlier but the travel rate between the dams (29 km/day) did not change. The difference in migratory pattern between the two river segments was surprising because similar decreases in flow and increases in temperature occurred at Bonneville, McNary, and Rock Island dams from 1954 to 1994. The faster travel rate in the lower than in the upper river (49 vs. 29 km/day) despite similar mean water velocities (25 vs. 23 km/day) may be related to fatigue or maturation by the fish, differential availability of low-velocity areas, configuration of the dams, or other factors.

There are several possible explanations for the changes in travel rate over the past decades. First, changes in fishing effort over the years could have caused apparent trends in sockeye passage dates at the dams. However, it seems unlikely that the increase in travel rate between Bonneville and McNary dams is an artifact of fishing because the correlations between travel rate and temperature and flow, and the correlations of the corresponding residuals, were so strong and consistent. The fishing pressure on sockeye salmon (Fryer 1995) has not been sufficiently great or steady to account for the progressive changes in timing. A change in the relative abundance of components of the sockeye salmon stock complex could also cause an apparent change in timing. However, the Wenatchee and Osoyoos populations have fluctuated without sufficient trend to account for the changes. Moreover, Snake River sockeye apparently pass McNary Dam earlier than the other populations, so their decline in recent years would likely make the 50% passage date at McNary Dam become slightly later, not earlier as was observed.

It is also possible that the salmon travel rate in the reservoirs has not changed but that changes in water management have affected the time needed to locate and ascend fish ladders at the dams. Use of Rock Island Dam fish ladders was influenced by patterns of spill and proximity to spillway gates (Leman and Paulik 1966). Ascent of fish ladders may be relatively rapid (3.6 h for nine sockeye salmon at Bonneville Dam: Ross 1983), but radio tracking studies at various dams indicated delays of 5–7 days below dams (e.g., Johnson et al. 1982; Ross 1983; Turner et al. 1984) and a positive association between spill and delay (Turner et al. 1983). This would be consistent with slower travel rates in the past. However, there was evidence that "zero" flow water storage conditions increased travel times between Lower Monumental and Little Goose dams, above Ice Harbor Dam on the Snake River (Liscom et al. 1985). These data suggested that very low velocities might delay salmon, but more recent tracking data indicated that chinook salmon ascended ladders and migrated through reservoirs rapidly (Bjornn et al. 1995; Stuehrenberg et al. 1995). The changing discharges and modifications in the dams themselves over the years make it difficult to determine the factors responsible for the increased travel rate in the lower river. However, changes associated with new dams constructed on the Bonneville Dam – McNary Dam river segment did not appear to have had a strong effect on the travel rate between these dams. The trend of increasing travel rate, although not as strongly correlated with flow and temperature conditions as it was for 1954–1994, was evident during the 1968–1994 period, when no new dams were constructed.

Osborne (1961) reported a negative correlation between discharge and travel rate between Bonneville and Rock Island dams and pointed out that the weaker currents might allow the

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Table 3. Linear regressions for the Bonneville Dam – McNary Dam and McNary Dam – Rock Island Dam river segments.

Relationship	Segment	Years	r^2	Slope	Intercept	p
Travel rate vs. year	BVL–MCN	1954–1994	0.38	0.67	21.6 km/day	<0.001
Travel rate vs. year	BVL–MCN	1968–1994	0.28	0.91	27.2 km/day	0.004
Travel rate vs. MCN temp	BVL–MCN	1954–1994	0.34	7.17	N/A	<0.001
Travel rate_{RES} vs. MCN temp_{RES}	BVL–MCN	1954–1994	0.20	4.77	N/A	0.004
Travel rate vs. MCN temp	BVL–MCN	1968–1994	0.31	7.84	N/A	0.003
Travel rate_{RES} vs. MCN temp_{RES}	BVL–MCN	1968–1994	0.19	5.70	N/A	0.024
Travel rate vs. MCN flow	BVL–MCN	1954–1994	0.41	–0.0028	N/A	<0.001
Travel rate_{RES} vs. MCN flow_{RES}	BVL–MCN	1954–1994	0.11	–0.0018	N/A	0.032
Travel rate vs. MCN flow	BVL–MCN	1968–1994	0.31	–0.0032	N/A	0.003
Travel rate_{RES} vs. MCN flow_{RES}	BVL–MCN	1968–1994	0.14	–0.0022	N/A	0.051
Travel rate vs. year	MCN–RID	1955–1994[a]	9×10^{-5}	–0.005	29.9 km/day	0.958
Travel rate vs. RID temp	MCN–RID	1955–1994[a]	0.04	1.44	N/A	0.257
Travel rate_{RES} vs. RID temp_{RES}	MCN–RID	1955–1994[a]	0.06	2.28	N/A	0.146
Travel rate vs. RID flow	MCN–RID	1955–1994[a]	0.03	–0.0004	N/A	0.382
Travel rate_{RES} vs. RID flow_{RES}	MCN–RID	1955–1994[a]	0.12	–0.0016	N/A	0.057

Note: Variables: sockeye salmon travel rates between dams (km/day), the mean daily temperature (°C) and discharge (m^3/s) for June 1 – July 31 (temp, flow), and swimming velocities against the water (km/day). Temperature and flow variables are preceded by MCN or RID to indicate that the data's source (McNary Dam or Rock Island Dam). Residuals of the above variables are denoted by subscript RES.

[a]Years with missing data.

sockeye salmon to ascend the river faster. Likewise, Gilhousen (1990) reported significant negative correlations between discharge of the Fraser River at Hope and travel rate to the spawning grounds of the Chilko and early Stuart populations. To understand the changes in sockeye salmon migration, one would like to determine not only their travel rate but also their speed against the water. This cannot be done reliably without direct information on the conditions experienced by the fish (e.g., Hinch et al. 1996). However, for comparative purposes, we estimated swimming speed by adding travel rate and water velocity estimates. The estimated sockeye swimming speed against the water between Bonneville and McNary dams decreased from 91 to 74 km/day from 1954 to 1994, and the estimated swimming speeds between McNary and Rock Island dams decreased from 115 to 52 km/day from 1955 to 1994. The decreased water velocity in the upper river may now allow the sockeye to swim slower than in the past but achieve similar travel rates relative to land. In contrast, the mean water velocity decreased by 44 km/day between Bonneville and McNary dams from 1954 to 1994, but the estimated sockeye swimming speed only decreased by 17 km/day. In this case, the sockeye may be swimming at similar speeds and traveling faster than in the past. It is unclear why the swimming speed would decrease less over the Bonneville Dam – McNary Dam segment than it did over the McNary Dam – Rock Island Dam segment.

The estimated swimming speeds were based on the assumption that the fish swam steadily against the mean velocity of the river. They probably swam in parts of the river with lower than average velocities, resulting in overestimates of swimming speed. Additionally, the changes in opposing water velocities may have been accompanied by changes in swimming behavior. Ellis (1962, 1966) reported that at water velocities <0.52 m/s (45 km/day), Sproat River sockeye generally swam steadily. At faster velocities, steady swimming was replaced by darting, alternated with position holding. In spite of these weaknesses, the swimming speed estimates indicate the opportunity for energetic savings provided by the reduced river discharge.

The least-cost speed for a 61-cm sockeye was 1.8 km/h, or 0.82 body lengths/s (Brett 1983). Using fork length-at-age and age composition data to determine average lengths for sockeye migrating to the Wenatchee and Okanogan rivers (Fryer 1995), and the relationship between fork length and total length (Brett 1967), this least-cost speed translates to an average of 40.9 km/day for the Lake Wenatchee population and 35.4 km/day for the Lake Osoyoos population. The average estimated swimming speeds over the two river segments for all years combined (82.5 km/day (3.4 km/h) for Bonneville to McNary and 81.6 km/day (3.4 km/h) for McNary to Rock Island) were roughly twice these least-cost speeds. The salmon would have to ascend the Columbia River continuously (24 h/day) in essentially slack water to accomplish the observed travel rates at their least-cost speed. In coastal waters, sockeye salmon swam 2.4 km/h, somewhat faster than their least-cost speed (Quinn 1988). Few salmon ascended the dams at night, and if they also swam slower at night, as they did in coastal waters (Quinn 1988), daytime speeds would have to increase to make good the same travel rate. Although our calculations may have overestimated the actual swimming speeds, Columbia River sockeye salmon are capable of impressive migratory performance. Collins et al. (1962) placed a 51-cm sockeye in an "endless fishway" with 1:8 slope and a lock to return the fish to the bottom. The fish swam for over 5 days, ascending the equivalent of 2025 m, without evidence of fatigue from blood lactate levels before it was removed from the apparatus.

The T_W trends indicated that, over the period of record, the temperatures experienced by sockeye salmon increased at Bonneville Dam (Quinn and Adams 1996), did not change significantly at McNary Dam, and decreased at Rock Island Dam. Temperature affects swimming performance (Brett 1967) but the data were inconsistent with the hypothesis that temperature changes directly affected swimming. Gilhousen (1990) reported a positive correlation between temperature and travel rate for two Fraser River sockeye populations, early Stuart and Chilko. These populations migrated upriver early

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in the season, when an increase in mean temperature along the migration route brought temperatures closer to the 15°C optimum for performance (Brett and Glass 1973; Brett 1995). In contrast, the T_W at the Columbia River dams were all above 15°C, so in this case, increased temperatures should decrease swimming performance and decreased temperatures should increase performance. Swimming performance should thus have decreased between Bonneville and McNary dams and increased between McNary and Rock Island dams, but the estimated swimming speed decreased in both segments. We do not know how temperature might affect volitional swimming speed in this case and this may have played a role in the patterns observed.

Upriver of the dams we studied, early arrival dates have been noted as well. Chapman et al. (1995) reported that sockeye salmon arrived at Tumwater Dam on the Wenatchee River almost 30 days earlier in 1994 than in 1935. On the Okanogan River at Zosel Dam, limited data also suggested earlier sockeye run timing (Chapman et al. 1995). While early arrival was observed at the various dams, the effect of this early arrival on the temperatures experienced by sockeye varied greatly among dams. At Bonneville Dam, the T_W increased from 1949 to 1993 (Quinn and Adams 1996). However, at McNary Dam the T_W did not change (1954–1994) and at Rock Island Dam it actually decreased (1933–1994) because increased river temperatures (most pronounced in the lower river) were offset by increased travel rates and earlier arrival upriver.

Lethal temperatures (above 24°C, Servizi and Jensen 1977) were almost never recorded at the dams, but sublethal temperatures could be detrimental to salmon by increasing susceptibility to disease (Colgrove and Wood 1966) or elevating metabolic demand (Brett 1995). Gilhousen (1990) found that Fraser River temperature during migration (and on the spawning ground) was positively correlated with prespawning mortality of female sockeye salmon. Indeed, this phenomenon was so well recognized that the fisheries were modified to take sockeye salmon whose survival was expected to be reduced by high temperatures and protect those later in the season that were expected to enjoy cooler water and higher survival rates (e.g., IPSFC 1962). Columbia River sockeye accomplish arduous migrations, presumably on limited energy reserves, as is the case for Fraser River sockeye (Gilhousen 1980). An increase in metabolic energy demand could divert energy away from other functions and affect survival or reproductive success. However, the reduction in mean temperature experienced by sockeye salmon in the upper river and the reduced river velocities may have resulted in energetic savings.

The effects of the shift toward an earlier arrival in the upper Columbia River on survival and reproduction are unknown. Sockeye salmon that reach Lake Wenatchee may find cool water below the thermocline, and limited evidence indicates that the dates of spawning have not changed markedly over the years (Chapman et al. 1995). The timing of upstream migration and spawning appear to be under separate control, which seems necessary because migration timing should be affected by the conditions experienced by the adult on the river whereas spawning should be timed to optimize the conditions that will be experienced by the progeny. Consistent with this hypothesis, our analysis of Gilhousen's (1990) data on Fraser River sockeye salmon revealed that migratory timing (measured at Hell's Gate) was significantly more variable than timing of spawning for the two populations with the longest records (Chilko River, 29 years; Stellako River, 26 years). Of the four populations with the longest records (Chilko, Stellako, Raft, and early Stuart), only Chilko showed a significant correlation between dates of migration and spawning.

The bimodal frequency distributions of sockeye passing Ice Harbor Dam in some years indicated delay. Based on inspection of the yearly temperature curves and passage dates at Ice Harbor Dam, migration usually ceased at temperatures above 21°C. A similar temperature block was documented for sockeye entering the Okanogan River at its confluence with the Columbia River (Major and Mighell 1967). In that case, increasing or stable Okanogan River temperatures above 21°C delayed migration whereas temperatures that were above 21°C but decreasing did not delay migration. If the salmon comprising the "late" mode at Ice Harbor Dam experience warmer temperatures than those migrating earlier, the energetic cost might reduce the probability of successful migration and reproduction. This possible problem may be mitigated somewhat by the observed reduction in maximum temperatures at Ice Harbor Dam, but so few sockeye salmon now ascend the Snake River that this may do little to help the population's recovery.

In summary, the Columbia River has been greatly changed by water management. Marked changes in fish behavior have accompanied the changes in flow and associated changes in temperature. These changes have led to faster upriver travel and earlier arrival dates for sockeye salmon, and varied effects on the temperatures experienced by the fish, depending on location in the river. We specifically studied sockeye salmon, whose migration has been advanced by the river's reduced flow and early spring warming. However, the later cooling of the river in fall might delay the migratory timing of other salmon species. It might also be important to determine the net effects of changes in migratory timing on the fitness of salmon, but these effects would be difficult to disentangle from other direct effects of hydroelectric development on the fish and indirect effects caused by the changes in the river's physical and biological attributes.

Acknowledgments

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Relating swimming performance of lake sturgeon, *Acipenser fulvescens*, to fishway design

S. Peake, F.W.H. Beamish, R.S. McKinley, D.A. Scruton, and C. Katopodis

Abstract: Fishways have traditionally been designed to provide safe passage for jumping fish and only recently have nonjumping species been considered. Concern over dwindling populations of lake sturgeon, *Acipenser fulvescens*, has focused attention on fishway designs that accommodate its swimming abilities. The objective of this study was to derive a model that relates swimming endurance of lake sturgeon to length and flow characteristics of fishways. Endurance at sustained and prolonged swimming speeds (those maintainable for more than 20 s) increased with water temperature but was independent of temperature at higher burst speeds. Endurance increased with total length at all swimming velocities. Swimming performance of lake sturgeon, relative to body length, is inferior to that of most salmonids, particularly at burst speeds. Fishway designers need to consider swimming ability, space requirements, and behavior of lake sturgeon to ensure that they can ascend potential migratory obstacles safely.

Résumé : Traditionnellement, les échelles à poissons ont été conçues pour permettre le passage sans danger des poissons capables de sauter et ce n'est que récemment que des espèces qui ne sautent pas ont été prises en considération. Les préoccupations concernant le déclin des populations d'esturgeons de lac, *Acipenser fulvescens*, ont attiré l'attention sur des échelles à poissons conçues pour accommoder ses capacités de nage. L'objectif de la présente étude était d'élaborer un modèle qui relie l'endurance à la nage de l'esturgeon de lac à la longueur et à l'écoulement des échelles à poissons. L'endurance à la nage prolongée et soutenue (qui peut être maintenue pendant plus de 20 s) a augmenté avec la température de l'eau, mais elle était indépendante de la température aux vitesses de pointe. L'endurance a augmenté avec la longueur totale à toutes les vitesses de nage. La performance de nage de l'esturgeon de lac, par rapport à sa longueur corporelle, est inférieure à celle de la plupart des salmonidés, particulièrement aux vitesses de pointe. Les concepteurs d'échelles à poissons doivent prendre en considération la capacité de nage, les besoins en espace et le comportement de l'esturgeon de lac pour s'assurer que ce dernier pourra franchir sans danger les obstacles potentiels à sa migration.
[Traduit par la Rédaction]

Introduction

Since the mid-1800's, populations of lake sturgeon, *Acipenser fulvescens*, have decreased dramatically due to commercial exploitation, loss of habitat, and an increasing sport fishery (Rochard et al. 1990). Slow growth, late sexual maturity, and infrequency of spawning all contribute to their vulnerability to exploitation (Brousseau 1987). In large rivers, hydroelectric installations can impede migrations and cause instability in flow rates, decreasing the quality of spawning and feeding habitat (Harkness and Dymond 1961; Auer 1996). Although fishways have been constructed on some rivers to allow safe passage of migratory fish, designs have been based primarily on the swimming capabilities of salmonids (Collins et al. 1962, 1963; Weaver 1963). Only recently have fishways been designed to accommodate other species (e.g., Katopodis et al. 1991).

Swimming ability among fish can vary with differences in anatomy and metabolism. Fishways designed to allow passage of one species can select against others of lesser ability (Schwalme et al. 1985). One difference that exists between sturgeon and salmonids is tail morphology. Salmonid tails are broad and homocercal whereas the tail of the lake sturgeon is heterocercal. The small lower lobe gives the sturgeon tail less depth, making its contribution to total thrust less than that of salmonids (Webb 1986). Sturgeon also produce more drag per unit of surface area than trout, presumably due to the presence of their bony plates or scutes (Webb 1986). Because drag increases with the square of velocity, high swimming speeds may impose a large energetic cost. Because routine metabolism of sturgeon has been found to be significantly lower than that of most teleost fishes (Singer et al. 1990), it may be that insufficient energy can be produced to attain the high speeds necessary to pass fishways designed for salmonid species.

Swimming activities of fish in general have been described by three categories: sustained, prolonged, and burst. Sustained occurs at relatively low velocities and represents speeds that can be maintained for a period greater than 200 min, making use of energy derived exclusively from aerobic processes (Beamish 1978). The velocity immediately below that that causes endurance to fall under 200 min is referred to as maximum

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sustained speed. Prolonged swimming covers a spectrum of speeds between sustained and burst. Burst represents high velocities that can be maintained for less than 20 s, using energy entirely generated by anaerobic processes (Beamish 1978). Sustained, prolonged, and burst speeds can be identified by measuring endurance over a range of swimming velocities. Endurance is defined as the amount of time a fish can swim at a particular speed.

Ideally, fishways should provide upstream passage for all migratory species inhabiting the river on which they are located. Water velocities within fishways should be less than the maximum attainable speed of all sizes and species that they are designed to pass, and the distance a fish must swim in the fishway should not exceed its endurance. The present study investigated swimming endurance of lake sturgeon in relation to body size and ambient temperature. Sustained, prolonged, and burst performance was compared with that of salmonids, and recommendations for future fishway designs capable of accommodating both species are offered.

Materials and methods

Lake sturgeon swimming performance was determined for individuals 12.0–132.0 cm in total length. A total of 58 sturgeon, 12–55 cm, were obtained as progeny of wild stock from the Moose River basin in northern Ontario. Five large fish, 106–132 cm, were captured in trap nets from southeastern Lake Huron. All fish were held in the laboratory in tanks supplied with running nonchlorinated well water. Sturgeon were subjected to a 16 h light : 8 h dark photoperiod. Small sturgeon (12–15 cm) were fed live earthworms to satiation three times per week, intermediate fish (23–55 cm) received daily feedings of dry pellet formula, and large fish (106–132 cm) were fed live crayfish (*Orconectes* sp.) to satiation three times per week.

Prior to experiments, water temperature was adjusted to 7.0, 14.0, or 21.0 ± 0.5°C by an increase of 1.0° or a decrease of 0.5°·day^{-1}. Before fish were used in experiments, they were held at the selected temperature for at least 7 days and were not fed for 36 h immediately prior to testing to ensure that they were in a postabsorptive state. Swimming performance of small sturgeon was measured in 3.2-L swimming flumes (Waiwood and Beamish 1978). Intermediate fish were tested in a 200-L swimming flume (Farmer and Beamish 1969) modified by the addition of a vertical chimney at the downstream end of the swim chamber through which fish were introduced and removed. Water velocity within the flumes was measured using a recently calibrated current meter and controlled by rheostats. Water flow within the 3.2- and 200-L swim flumes was essentially rectilinear and even across the profile. Water from aerated and thermally controlled reservoirs was added at a rate of approximately 120 and 600 mL·min^{-1} for the 3.2- and 200-L flumes, respectively, to assure oxygen content in excess of air saturation and a constant temperature.

Performance of large sturgeon was measured in a black PVC pipe approximately 2.5 m long with a diameter of 56 cm. The tube was equipped with a fixed plastic retaining screen at the upstream end and a removable rubber mesh screen at the downstream end. Fish were introduced and removed at the downstream end of the tube. Two windows (15 × 25 cm) were cut in the apparatus about 0.5 m from each end to facilitate viewing of fish. Windows were covered from the inside with heavy-gauge clear vinyl to minimize internal turbulence. Strips of white tape were applied to the inside of the tube, in the window regions, to allow fish to be seen against the dark interior. After assembly, the entire apparatus was submerged and secured within a large aquatic flume (3 × 5 m) located at the University of Guelph, Guelph, Ont. Flow was found to be essentially rectilinear and flow rates were calibrated. Maximum cross-sectional areas of all lake sturgeon used in this study were less than 10% of that of their respective swimming flumes, eliminating the need to adjust for blocking effect (Smit et al. 1971).

Performance was evaluated by measuring swimming endurance. Fish were transferred from a holding tank to a flume and allowed to swim at approximately 0.45 body lengths (bl)·s^{-1} for 1 h, after which velocity was abruptly increased to the desired test velocity. Endurance was measured at velocities of 20, 40, 45, and 50 cm·s^{-1} for small fish, ranging from 30 to 90 cm·s^{-1} for intermediate sturgeon, and 90, 120, 150, and 180 cm·s^{-1} for large fish. Small, intermediate, and large sturgeon were unable to swim at speeds greater than 50, 90, and 180 cm·s^{-1}, respectively. Small fish were tested at 7.0 and 14.0°C, intermediate sturgeon at 7.0, 14.0, and 21.0°C, and large fish at 14.0 ± 0.5°C. Velocities that resulted in endurance responses greater than 200 min were considered to represent sustained swimming. To ensure that sturgeon could maintain these speeds indefinitely, fish that swam in excess of 200 min were allowed to continue for an additional 280 min after which the experiment was terminated. Because these fish did not fatigue, but were interrupted, these data were not used in the development of the endurance model. Swimming endurance was estimated using multiple regression (Draper and Smith 1966) as follows:

$$\log(E) = a_0 + a_1L + a_2T + a_3V + a_4LT + a_5TV + a_6LV + a_7LTV + e$$

where E is endurance (minutes), L is total length (centimetres), T is water temperature (degrees Celsius), V is swimming velocity (centimetres per second), and e is a normally distributed error term with mean 0 and variance σ^2. Values of P less than 0.05 indicated statistical significance.

Accurate measurements of swimming endurance depend on consistent recognition of fish fatigue. Electric shocking was not used in this study. Instead, fish were occasionally stimulated to maintain swimming by various methods, depending on the flume in which they were tested. Small fish were completely enclosed in the flume and were stimulated by short and sharp fluctuations in velocity followed by an immediate return to the test velocity. Intermediate fish, in the 200-L flume, were stimulated by gentle prodding with a plastic rod and by velocity fluctuations as described for small fish. Large sturgeon were also gently prodded to keep them from resting against the downstream retaining screen. In all cases, fish were considered fatigued when they became impinged on the downstream screen and failed to resume swimming despite repeated attempts to stimulate them. In most cases, onset of fatigue was obvious. After an experiment, fish were measured, weighed, and returned to their holding tanks. All fish were allowed to recover for at least 48 h prior to being used in another swim test at a different velocity.

Results and discussion

Swimming performance

Swimming endurance of lake sturgeon, in general, was found to increase with fish length at all swimming speeds and temperatures tested. Large fish could swim for longer and attain higher speeds than smaller fish. Swimming velocities that sturgeon could maintain for more than 200 min were considered to represent sustained speeds. The highest velocity that did not eventually result in fatigue represented maximum sustained speed for that fish. This speed can only be approximated experimentally, but was also found to increase with fish length.

The relationship between endurance, water temperature, fish length, and swimming speed is described by the regression

$$(1)\quad \log(E) = 1.40 + (2.26 \times 10^{-2} \times L) + (5.47 \times 10^{-2} \times T) - (4.55 \times 10^{-2} \times V) - (5.36 \times 10^{-4} \times T \times V) + (1.85 \times 10^{-4} \times L \times V).$$

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The model has a critical F-value of 274.6 ($P < 0.05$), an adjusted r^2 of 0.854, and 233 degrees of freedom. Interactions between temperature and length and between temperature, velocity, and length were not significant.

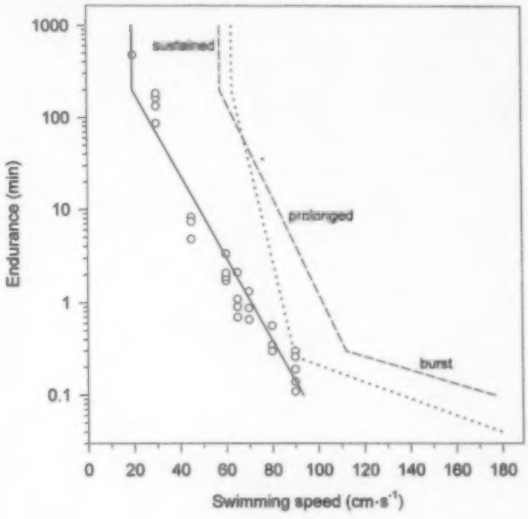
Fatigue curves are important tools in studies of fish swimming performance and, for lake sturgeon, can be generated by plotting endurance (calculated from equation 1) against a range of swimming speeds on a semilog graph. Fatigue curves, for salmonids, are characteristically resolved into three straight sections connected by two changes in slope (Fig. 1). The first section is vertical and is located at maximum sustained speed. Swimming speeds to the left of this section are considered sustained. The change in slope that occurs at maximum sustained speed marks the beginning of the second section which represents prolonged swimming. The second inflection typically occurs at a speed that results in fatigue after 20 s. This slope change marks the beginning of the third section representing burst swimming speeds.

Fatigue curves generated for lake sturgeon take the form of a single straight line with no change in slope between prolonged and burst swimming (Fig. 1). The line represents endurance for fish of a prescribed total length (12.0–132.0 cm), at a given temperature (7.0–21.0°C), at speeds greater than maximum sustained. It is not valid for endurance responses greater than 200 min. A vertical line must be added, at maximum sustained speed, to reflect the demonstrated ability of lake sturgeon to swim indefinitely at sustained velocities. This model is also not valid for determining endurance for fish greater than 55 cm long at temperatures other than 14°C, or for fish less than 23 cm long at temperatures greater than 14°C. A temperature of 14°C, for large sturgeon, should be appropriate for application to migrating fish which generally spawn when water temperatures are in the 11–16°C range (Table 1). Nevertheless, peak spawning has been observed at temperatures as low as 8.5°C (Kempinger 1988) and, in these cases, equation 1 may overestimate actual swimming capability.

Fatigue curves indicate that large sturgeon can swim longer and at higher speeds than smaller fish (Fig. 2). Sturgeon, 120 cm in length, at 14°C, can swim for 127.5 min at 90 cm·s^{-1}, whereas 45-cm fish can maintain this speed for just 8.7 s. Maximum sustained speed also increases with length, from 4.0 cm·s^{-1} for 15-cm sturgeon to 83.7 cm·s^{-1} for 120-cm fish at 14°C. Endurance declines rapidly, for fish of all sizes, at velocities greater than their maximum sustained speed. A sturgeon 45 cm in length, at 14°C, can swim for 194.6 min at 20 cm·s^{-1}, but will fatigue after 8.7 s at 90 cm·s^{-1}.

Water temperature was also found to affect lake sturgeon swimming ability. Maximum sustained speed for a 45-cm fish increases with temperature, from 12.0 cm·s^{-1} at 7°C to 26.0 cm·s^{-1} at 21°C. This allows swimming categories for the same fish to change with a fluctuation in water temperature. The 45-cm sturgeon, swimming at 25.0 cm·s^{-1} and 7°C, fatigues after 59.8 min, indicating prolonged swimming, but at 21°C, the same fish can maintain 25.0 cm·s^{-1} for longer than 200 min, indicating sustained swimming. Endurance is also enhanced by temperature at prolonged speeds. Endurance of a 45-cm fish, swimming at 30 cm·s^{-1}, increases with temperature, from 37.3 to 129.6 min at 7 and 21°C, respectively. The magnitude of the temperature effect is most pronounced at speeds just above maximum sustained, and decreases as velocity increases, eventually becoming inconsequential at high speeds. The 45-cm sturgeon swimming at 90 cm·s^{-1} will fatigue after 7.8 s at 7°C and after 9.7 s at 21°C.

Fig. 1. Comparison of fatigue curves for lake sturgeon (solid line), Arctic char, *Salvelinus alpinus* (dashed line), and rainbow trout, *Oncorhynchus mykiss* (dotted line) showing sections for sustained, prolonged, and burst swimming. Circles represent data for medium-sized sturgeon at 14°C. The fatigue curve for sturgeon was determined using a length value of 45 cm, a temperature of 14°C, and a range of swimming speeds (20–95 cm·s^{-1}) substituted into equation 1. Positions of fatigue curves for rainbow trout (24 cm) and Arctic char (34 cm) were determined by Bainbridge (1960, 1962) and Beamish (1980), respectively.



In general, lake sturgeon do not become sexually mature until they reach lengths of 100–150 cm (Table 1). From equation 1, a 130-cm fish can maintain position indefinitely in flows up to 96.8 cm·s^{-1}, and they can swim for shorter periods at speeds up to 180 cm·s^{-1}. These findings agree well with published reports concerning flow rates in areas where lake sturgeon spawn (Table 1).

Comparisons with salmonids

Patterns in lake sturgeon fatigue curves resemble those found for salmonids with some noteworthy exceptions. Curves representing sturgeon endurance do not show the second inflection corresponding to burst swimming. Endurance, at high speeds, simply continues to decline at the same rate as for prolonged speeds (Fig. 1). Consequently, it appears that lake sturgeon are not capable of attaining the high burst speeds that salmonids can typically achieve. This, however, is not to say that lake sturgeon do not possess burst swimming capability. Many species, whose performance has been shown to be affected by temperature, show the effect most profoundly at sustained and prolonged speeds, but not at burst (Brett 1964; Beamish 1978). Lake sturgeon endurance is similarly influenced by temperature, showing enhanced sustained and prolonged performance at higher temperatures, but an independence from temperature at speeds that can be maintained for less than 20 s. It is therefore probable that, at a

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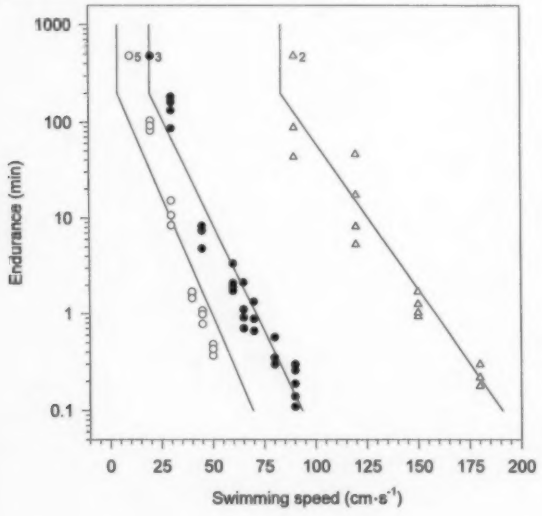
Table 1. Published values of flow speed, water temperature, and fish length at the time of sturgeon spawning (a dash indicates that the corresponding information was not provided).

Location	Flow speed ($m \cdot s^{-1}$)	Water temperature (°C)	Fish length (cm)	Source
Wolf River, Wisconsin, U.S.A.	>0.10	8.3–16.1	—	Kempinger 1988
Des Prairies River, Quebec, Canada	0.02–1.09	11.6–15.4	—	LaHaye et al. 1992
L'Assomption River, Quebec, Canada	0.4–1.39 (0.61–0.84)[a]	11.0–21.5	—	LaHaye et al. 1992
Southern Quebec, Canada	—	—	116.8	Roussow 1957
Sturgeon River, Michigan, U.S.A.	—	10–15	153.9	Auer 1996

[a]Flows containing the highest egg concentrations.

Fig. 2. Relationship between length, endurance, and swimming speed of lake sturgeon. Open circles, solid circles, and open triangles represent data from small, intermediate, and large fish, respectively. Positions of fatigue curves (from left to right) were determined using length values of 15, 45, and 120 cm, swimming speeds of 4–190 $cm \cdot s^{-1}$, and a temperature of 14°C substituted into equation 1. The number against each line (top) indicates the number of fish tested.



physiological level, these velocities represent burst swimming for lake sturgeon.

The poor swimming performance of sturgeon, relative to that of salmonids, is not confined to burst speeds but is evident in all categories of swimming. Studies of sturgeon physiology have found that metabolism is intermediate between the more primitive elasmobranch and the more advanced teleost fishes (Singer et al. 1990). A lower overall metabolism could partially account for the depressed swimming ability of lake sturgeon. Disproportionately poor performance at burst swimming speeds may also indicate that anaerobic processes used by sturgeon are less efficient at providing usable energy than those in salmonids. Further, the apparent absence of a change in slope, at burst speeds, may indicate a more gradual shift to exclusive anaerobic metabolism than that demonstrated by salmonids.

Morphology, and specifically that of the tail, can also significantly influence swimming capabilities among fish species. The salmonid tail is symmetrical, with upper and lower lobes producing similar thrust; however, the lower lobe of the sturgeon tail is smaller than the upper and consequently generates 66% less thrust than the lower tail lobe of similarly sized trout (Webb 1986). The net effect is that the sturgeon tail, as a whole, generates 18% less thrust than that of trout over sustained and prolonged speeds (Webb 1986). The consequences of lower thrust are further complicated by morphological differences in body form between sturgeon and salmonids. Salmonids have smooth, streamlined bodies whereas sturgeon have a rough surface and a less fusiform shape. Studies have found that the drag generated by a sturgeon is approximately 3.5 times that of a trout of equal surface area (Webb 1986). This means that a sturgeon must generate more thrust, with its less efficient tail, than a trout and will require more energy to maintain the same swimming speed. Anaerobic metabolism, at burst speeds, provides a limited amount of energy that the sturgeon will likely use up faster than the trout, resulting in reduced burst performance.

Applications to fishways and culverts

Traditionally, fishways have been installed to provide safe passage for economically valuable salmonids, with little regard for other migratory species such as the lake sturgeon. If fishways are to be successful, fish must be able to ascend them quickly; therefore, prolonged and burst swimming capabilities are of primary importance in establishing suitable water velocities within the structures. Unfortunately, lake sturgeon swimming performance differs most from that of salmonids at burst speeds. For both species to use a fishway, water velocities must be maintained within the swimming performance characteristics of sturgeon, it being the weaker swimmer.

It must also be stressed that most studies, including this one, determine swimming performance using flumes where swimming speed is equal to water velocity. Fish ascending a fishway or culvert must attain positive ground velocity, which requires them to swim faster than the water velocity in the fishway. A formula can be used to determine water velocities that will allow sturgeon to ascend fishways, given the length of the fishway and the minimum size of fish to be passed:

$$(2) \quad V_f = V_s - (d \times E_{V_s}^{-1})$$

where V_f is the water velocity within the fishway (centimetres per second), V_s is the swimming speed of the minimum-sized sturgeon (centimetres per second), d is the length of the fishway (centimetres), and E_{V_s} is the endurance of the sturgeon swimming at V_s (seconds). E_{V_s} can be determined using equation 1.

The maximum fishway water velocity that is suitable for sturgeon passage can be determined using the second derivative of equation 2. This velocity can also be estimated by solving equation 2 for various values of V_s and plotting V_s on the x-axis and V_f on the y-axis. An example of this graphical

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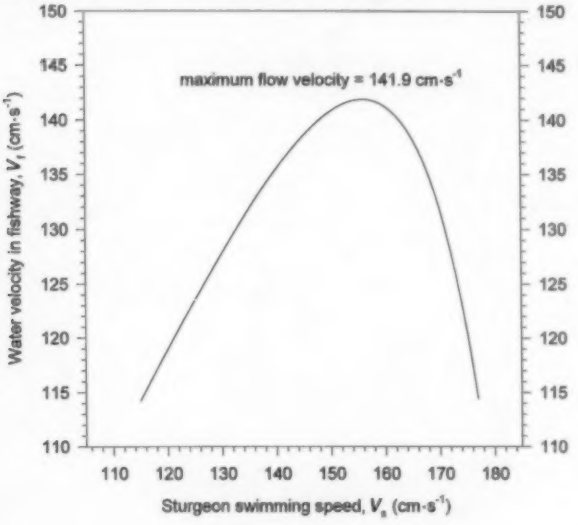
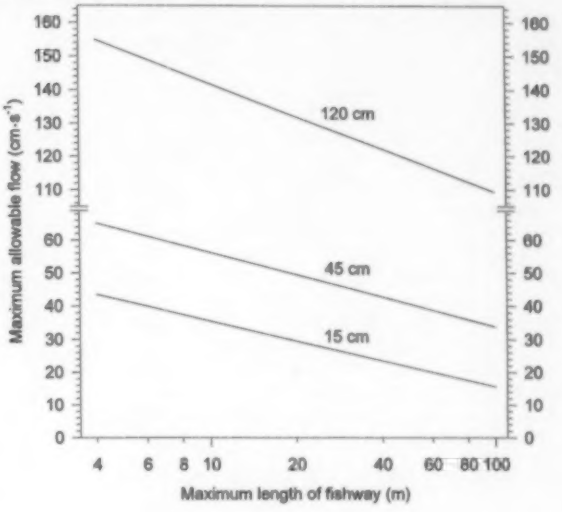
Fig. 3. Curve describing the swimming speeds required for a 120-cm lake sturgeon to successfully pass a 10-m fishway at 14°C. This curve was developed by substituting the appropriate values into equations 1 and 2. Under these circumstances, a 120-cm fish would not be expected to pass the fishway if flows within it exceeded 141.9 cm·s^{-1}. Different values of fish length, water temperature, and fishway length will yield different maximal values.



method is given in Fig. 3. Using this approach, maximum suitable velocity will correspond to the highest value of V_f on the resulting curve (141.9 cm·s^{-1} in Fig. 3). If water velocity were to be set at 141.9 cm·s^{-1}, the 120 cm sturgeon would have to maintain a speed of 156 cm·s^{-1} to successfully ascend the 10-m fishway. If, however, the velocity were set lower than maximum, for example at 135 cm·s^{-1}, the fish would be able to swim at speeds ranging from 140 to 168 cm·s^{-1}, thus creating a greater margin for error. Curves generated using equation 2 will change with temperature and fish length. Therefore, it is important, in determining E_{Vs}, to use temperatures and lengths that reflect those of migrating lake sturgeon (Table 1). Fishway length and maximum water velocity combinations that are suitable for passing small, intermediate, and large sturgeon at 14°C are given in Fig. 4.

Finally, it is important to note that mature sturgeon can be much larger than salmonids utilizing the same fishway. This means that swimming performance of large spawning sturgeon may be similar to that of smaller salmonids. Therefore, if emphasis is to be placed on passing mature sturgeon, the physical dimensions of the structure may be more important than water velocity. Fishway designs requiring fish to jump from step to step are not generally conducive to the passage of sturgeon. If, however, the goal in establishing the fishway is to provide safe passage for sturgeon, regardless of size, then slowing water velocity becomes important to successful passage. If sturgeon populations are to recover in the future, it is important that they have access to the type of habitat utilized prior to construction of roads, hydroelectric dams, and other river impediments. If fishways and culverts are to accomplish this, new designs must reflect the unique swimming capabilities of the lake sturgeon.

Fig. 4. Lines representing the maximum flows that would allow 15-, 45-, and 120-cm lake sturgeon to pass fishways 4–100 m in length at 14°C.



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Effects of base addition and brook trout (*Salvelinus fontinalis*) introduction on the plankton community of an acidic Adirondack lake

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Abstract: Calcite was added to Woods Lake in 1985 and 1987, and to its watershed in 1990, to restore and maintain water quality conditions suitable for reestablishing brook trout (*Salvelinus fontinalis*). Juvenile and adult brook trout were introduced following the first chemical treatment and were stocked annually thereafter from 1985 to 1989. In response to the combined chemical and biological manipulation, phytoplankton abundance increased whereas production per unit of biomass decreased. We attribute the increase in phytoplankton abundance and the reduction in biomass turnover rates to a decrease in zooplankton grazing. Zooplankton densities and estimated community grazing rates were lower during the posttreatment period despite a shift from small-bodied taxa (*Diaptomus minutus*, *Bosmina longirostris*) to a more diverse assemblage that included four species of daphnids. We attribute reductions in zooplankton abundance to planktivory of introduced brook trout. The changes we observed in phytoplankton and zooplankton species composition were consistent with trends observed during whole-lake acidification experiments, but functional responses in our experiment (decreased zooplankton abundance, increased phytoplankton abundance) were not. Our functional responses were consistent, however, with those observed previously in food webs manipulated to increase planktivore abundance.

Résumé : On a ajouté de la calcite dans le lac Wood en 1985 et 1987 ainsi que dans son bassin versant en 1990 pour rétablir et maintenir des conditions de qualité de l'eau qui permettent la réimplantation de la truite mouchetée (*Salvelinus fontinalis*). Des truites mouchetées adultes et juvéniles ont été introduites après l'application du premier traitement chimique, puis on a renforcé cette population annuellement de 1985 à 1989. Consécutivement aux manipulations chimiques et biologiques combinées, l'abondance du phytoplancton a augmenté alors que la production par unité de biomasse a diminué. Nous attribuons l'augmentation de l'abondance du phytoplancton et la réduction du taux de renouvellement de la biomasse à une diminution du broutage par le zooplancton. Les densités et les taux de broutage estimés de la communauté de zooplancton étaient plus faibles au cours de la période post-traitement en dépit du fait qu'on soit passé de taxons de petite taille corporelle (*Diaptomus minutus, Bosmina longirostris*) à un assemblage plus diversifié qui comprend quatre espèces de daphnidés. Nous attribuons les réductions touchant l'abondance du zooplancton à l'activité planctonophage de la truite mouchetée. Les changements que nous avons observés dans la composition des espèces de phytoplancton et de zooplancton concordaient avec les tendances observées durant les expériences d'acidification de lacs entiers, mais ce n'était pas le cas des réactions fonctionnelles dans notre expérience (diminution de l'abondance du zooplancton, augmentation de l'abondance du phytoplancton). Cependant, nos réactions fonctionnelles étaient en accord avec celles qui ont été observées antérieurement dans les réseaux alimentaires manipulés de manière à augmenter l'abondance des organismes planctonophages.
[Traduit par la Rédaction]

Introduction

Atmospheric deposition of strong mineral acids has significantly altered the chemical and biological characteristics of surface waters in sensitive regions of North America (Dillon et al. 1987; Schindler 1988; Baker and Christensen 1991). Biotic responses to acidification have been attributed to changes in lake chemistry, particularly elevated concentrations of toxic monomeric aluminum (Driscoll et al. 1980), and to changes in predator–prey interactions associated with the decline of planktivorous and piscivorous fish (Schofield 1976; Eriksson et al. 1980). Plankton communities have been among the most intensively studied groups of organisms in acidified lakes (Sprules 1975; Roff and Kwiatkowski 1977; Yan and Strus 1980; Keller and Pitblado 1984; Confer et al. 1983; Siegfried et al. 1988; Brett 1989; Locke 1992). There is a general concurrence that species richness in both phytoplankton and zooplankton communities decreases with increasing lake acidity. These shifts in species composition have been shown to follow consistent patterns across a wide range of experimental scales (from small enclosures to whole-lake experiments) and among lakes that differ in their geographic setting. Changes in phytoplankton communities are characterized by the decline of chlorophytes, chrysophytes, and diatoms, with an increase in dominance by large algal cells, particularly dinoflagellates

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(Almer et al. 1978; Yan 1979; Stokes 1986). In contrast, shifts in zooplankton community composition result in increases in the relative abundance of rotifers and small-bodied crustaceans such as *Diaptomus minutus* and *Bosmina longirostris* (Sprules 1975; Keller and Pitblado 1984; Pinel-Alloul et al. 1990). Large-bodied crustaceans, especially large daphnids, are generally absent from acidic waters (Sprules 1975; Siegfried et al. 1989; Keller et al. 1990; Havens 1992). Trends reported from lake survey data are generally consistent with changes in plankton communities during lake acidification experiments (Schindler et al. 1991).

Changes in community composition have important implications for phytoplankton–zooplankton interactions. Yan and Strus (1980) hypothesized that shifts in zooplankton size structure during acidification may reduce their grazing efficiency. Small cladocerans and rotifers graze a narrower particle size spectrum than large daphnids (Burns 1968) and also have lower absolute filtering rates (Porter et al. 1983). Therefore, community grazing rates may be lower in acid lakes dominated by small-bodied zooplankton and large phytoplankton. Havens (1992) observed decreases in the ratio of zooplankton to algal production corresponding to decreases in zooplankton body size and increases in algal cell size in experimentally acidified lake mesocosms. More recently, Blomqvist (1996) has suggested that moderately acidified lakes (pH 5–6) are often dominated by inedible cyanobacteria (*Merismopedia tenuissima*) that represent an energetic "dead-end" within the pelagic food web. Contrary to this hypothesis, results from whole-lake acidification experiments have not demonstrated substantial changes in zooplankton grazing rates and phytoplankton abundance (Sierszen and Frost 1990; Schindler et al. 1991). Furthermore, results from lake surveys have not shown consistent correlations between lake acidity and phytoplankton or zooplankton abundance (Dillon et al. 1984; Yan 1986).

This paper describes 9 years of plankton data collected at a lake that had undergone substantial changes in pH and food web structure following limestone addition and brook trout (*Salvelinus fontinalis*) introduction. The addition of calcitic limestone (commonly referred to as liming) is a widely practiced technique to improve water quality by neutralizing acidity and decreasing the solubility of toxic trace metals. The intent is to restore or preserve native fish stocks in regions where acidic deposition has altered water quality and affected acid-sensitive species. Calcite addition is often carried out in conjunction with other restoration efforts (fish stocking, phosphorus addition) to promote the development of sport fish populations. Effects of liming on plankton communities have been studied at a number of sites in Canada, the United States, and Sweden (reviewed by Olem 1991). In general, it has been shown that liming fosters a shift in species composition from assemblages dominated by a few acid-tolerant taxa to assemblages more closely resembling those of circumneutral lakes of comparable trophic state (Eriksson et al. 1983; Stokes 1986; Bukaveckas 1989; Molot et al. 1990). Based on results from previous lake liming and acidification studies, we proposed three hypotheses predicting the effects of the chemical treatment on phytoplankton–zooplankton interactions. We predicted that (1) an increase in lake pH would foster a more diverse zooplankton assemblage that included acid-intolerant species such as large grazers, (2) the presence of large, herbivorous zooplankton would result in higher community grazing rates, and (3) higher zooplankton grazing rates would increase biomass turnover of phytoplankton (higher biomass-specific production rate). We could not a priori postulate the effects of the concurrent food web manipulation due to uncertainty regarding the reproductive success of introduced brook trout and their feeding habits in lake environments. Brook trout were thought to feed primarily on macroinvertebrates and smaller fish (of their own species when stocked alone), and therefore, we did not anticipate the high rates of planktivory subsequently observed.

Our previous work had shown that the manipulation resulted in a decrease in water column transparency (Bukaveckas and Driscoll 1991*a*), stronger thermal stratification (Bukaveckas and Driscoll 1991*b*), and changes in the quantum efficiency of phytoplankton photosynthesis (Bukaveckas 1993). Shifts in phytoplankton and zooplankton communities during the first 3 years of the experiment were described by Bukaveckas (1989) and Schaffner (1989) and are summarized briefly here. Within 2 months after the manipulation, phytoplankton species composition shifted from a community dominated by a few acid-tolerant taxa to a more diverse assemblage characteristic of nonacidic lakes in the region. The posttreatment assemblage was dominated by a diverse group of taxa that included chlorophytes (*Chlorogonium*, *Elakatothrix*, *Schroderia*, and *Kirchneriella*), chrysophytes (*Uroglena* and *Synura*), and planktonic diatoms (*Synedra*). With the exception of *Dinobryon bavaricum*, most taxa comprising the pretreatment assemblage (*Gymnodinium*, *Mallomonas*, *Peridinium*, and *Merismopedia*) were absent or present at lower densities during the posttreatment period. Prior to calcite addition, the zooplankton community of Woods Lake was dominated by three species of herbivorous zooplankton (*Keratella taurocephala*, *D. minutus*, and *B. longirostris*) and a predatory cyclopoid copepod (*Mesocyclops edax*). Together, these four taxa comprised 92% of total density during the premanipulation period (Schaffner 1989). The community was typical of clearwater acidic lakes in the Adirondacks and other regions (Brett 1989; Havens and Hanazato 1993). Here, we focus on long-term trends in chlorophyll concentrations in relation to changes in zooplankton grazing. A number of issues pertaining to liming as a lake management strategy were addressed in this study, and those directly related to phytoplankton–zooplankton dynamics (lake versus catchment applications and effects of reacidification) are discussed.

Site descriptions and treatment design

Plankton communities were monitored at both the treated site (Woods Lake) and a nearby reference site (Dart's Lake) during nine summers (1984–1992). Site characteristics have been described elsewhere (Staubitz and Zarriello 1989; Driscoll et al. 1996) and are summarized briefly here. The lakes are located in the west-central Adirondack Mountains in predominantly forested and unpopulated watersheds. Woods Lake was selected as the principal site for the lake and watershed liming study because it exhibited chemical and biological characteristics typical of clearwater acidic lakes in this region (Driscoll and Newton 1985). Nearby Dart's Lake was selected as a reference site because of its similarity to Woods Lake and because extensive background data were available (Effler et al. 1985; Schafran and Driscoll 1987; Schofield and Driscoll

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1987). Woods Lake and Dart's Lake are similar in surface area (23 and 57 ha, respectively) and maximum depth (12 and 15 m, respectively). The sites differ in that Dart's Lake receives significant inflow from Big Moose Lake and has a shorter water residence time (85 days) compared with Woods Lake (180 days). Prior to treatment, the chemical characteristics of Woods Lake and Dart's Lake were similar. At both sites, sulphate was the dominant anion and the equivalence of acidic anions exceeded base cations resulting in low pH (4.9–5.5), reduced acid-neutralizing capacity (–15 to +20 μequiv.·L^{-1}), and high concentrations of monomeric aluminum (2–12 μmol·L^{-1}).

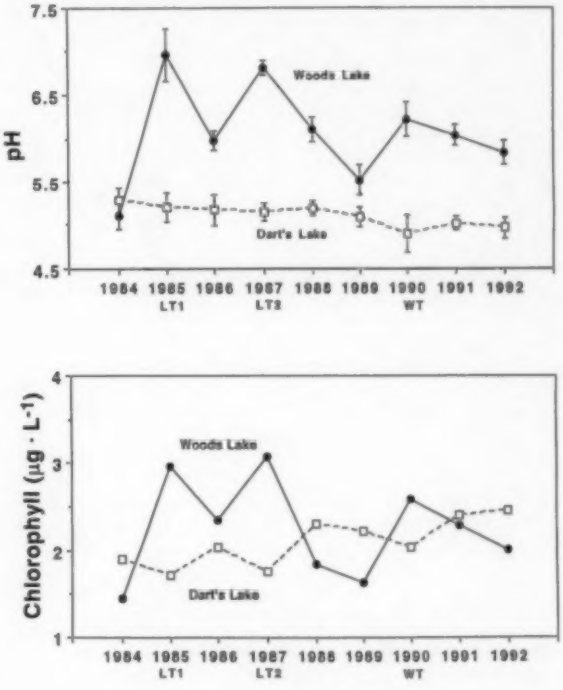
Data collected at Woods Lake included 1 year of pretreatment data, 5 years of data collected while elevated pH was maintained by adding calcite directly to the lake, and 3 years of data collected following application of calcite to the watershed. An account of the lake and watershed treatments and their effects on lake chemistry is presented in Driscoll et al. (1989*a*, 1989*b*, 1996) and will be summarized briefly. Following 1 year of baseline data collection (1984), Woods Lake was treated in May 1985 with an application of a highly pure calcite slurry that was added on a volumetric basis to achieve a uniform target pH (hereafter, lake treatment 1 (LT1)). The treatment resulted in an increase in summer mean pH from 5.1 in 1984 to 7.0 in 1985 (Fig. 1). Some reacidification was evident during the following summer (pH = 6.0 in 1986) and a larger dose of limestone was added in September 1986 (hereafter, lake treatment 2 (LT2)). The second treatment resulted in an increase in pH to 6.8 (1987) and thereafter the lake was allowed to reacidify for 3 years (to pH = 5.5) (Fig. 1). During the fall of 1989, calcite was applied to two subcatchments comprising 50% of the Woods Lake watershed (hereafter, watershed treatment (WT)). The watershed application resulted in a more moderate increase in lake pH (to 6.2 in 1990) and relatively little reacidification was apparent in the 3 years following treatment (Fig. 1).

Brook trout had been historically present in Woods Lake (Gloss et al. 1987) and were reintroduced following the first lake treatment (LT1) with an initial stocking of 1200 age 1+ and 5000 age 0+ individuals (Schofield et al. 1991). The lake was restocked with age 1+ brook trout in 1986 and 1987 (670 and 600 individuals, respectively) and age 0+ brook trout in 1988 and 1989 (8000 and 6000 individuals, respectively). No further stocking was attempted after 1989. The brook trout population was inventoried each spring and fall from 1985 to 1991 by trap netting (see Gloss et al. 1989 for methods). No other fish species were present in the lake or its tributary streams during the period of study.

Methods

Data were collected at the treated and reference lakes from 1984 to 1992. Chemical analyses included depth profiles of pH, cations, anions, and nutrients sampled at 3-week intervals throughout the year (Driscoll et al. 1996). Chlorophyll and primary production were measured during summer stratification (May–September) at 10- and 20-day intervals, respectively. Water samples were taken at 2-m intervals from the surface to the bottom at the deepest portion of the lake basin. Samples for chlorophyll analyses were processed within 1–2 h of collection by filtration through Gelman A/E glass fiber filters and extraction in 10 mL of aqueous (90%) acetone. Filters were macerated using a Teflon tissue grinder and steeped for 12 h in the dark at

Fig. 1. Interannual variation in pH and chlorophyll at the treated (Woods Lake) and reference (Dart's Lake) sites. Values for each year represent an average of volume-weighted estimates for the period from May through September. LT1, LT2, and WT denote the lake and watershed treatments.



4°C. Extracts were analyzed using a Varian DMS 70 spectrophotometer equipped with long-path-length (4 cm) cells and narrow (1 nm) bandwidth. Concentrations of chlorophyll degradation products were determined by measuring the optical density of the extract before and after acidification with 0.1 M HCl. Estimates of chlorophyll *a* corrected for phaeophytin *a* were calculated using the Lorenzen equations as modified by Speziale et al. (1984).

Phytoplankton productivity was measured using the ^{14}C isotope technique according to methods described in Bukaveckas (1993). Light and dark bottles were incubated for 4 h at midday (10:00–14:00) at three depths (3, 7, and 11 m) approximating the epilimnetic, metalimnetic, and hypolimnetic regions. Samples were collected using a nonmetallic Kemmerer sampler and incubated in 300-mL BOD bottles. Each bottle was injected with 5 μCi (1 Ci = 37 GBq) of radiocarbon as sodium bicarbonate. After incubation, samples were placed on ice and kept dark during transport to the laboratory (<1 h). Labeled phytoplankton were collected on Millipore HA membrane filters (0.45 μm) under low vacuum pressure. Filters were rinsed with acidified water and placed in scintillation vials containing 0.1 mL of 1 M HCl to remove unincorporated isotope (Lean and Burnison 1979). After 2–3 h, fluor was added (Aquasol-2, New England Nuclear Products) and activity was measured in a Beckman LS-233 liquid scintillation counter. Quenching was corrected by the external standard channels ratio technique. Dissolved inorganic carbon concentrations were measured by acid purging and infrared detection of CO_2 (Dorhmann 1984).

Zooplankton samples were collected at 3-week intervals from January 1984 through December 1989. Daytime tows were collected using a 30-cm-diameter net with an 80-μm mesh size and a 5:1 length to diameter ratio. Tows were started at 1 m above the bottom, and

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sample volume was estimated from the area of the net mouth and the length of the tow. About 300–500 individuals were counted from each of two replicate tows in a Bogorov counting tray at 60× magnification. Body lengths were measured for a minimum of 20 individuals of each major taxon for all sampling dates.

Community grazing rates were derived from species abundance data and published estimates of species-specific grazing rates. The equations of Sierszen and Frost (1990) were used to estimate grazing rates for dominant herbivorous zooplankton (*K. taurocephala*, *Bosmina*, *Daphnia*, and *D. minutus* adults and copepodites). The equations were derived from measured (in situ) grazing rates for the same taxa in a softwater, oligotrophic lake (Little Rock Lake) in northern Wisconsin. In Little Rock Lake, species-specific grazing rates were unaffected by changes in pH during experimental acidification from 6.2 to 5.2. Therefore, these equations were applied to data collected both before and after calcite treatment to derive species-specific grazing rates (millilitres per individual per hour) as a function of lake temperature (average water column temperatures in Woods Lake on dates when zooplankton tows were collected). Because Sierszen and Frost (1990) did not measure grazing by *D. minutus* nauplii, data from Bogdan and Gilbert (1984) were used. Both studies measured feeding rates using *Chlamydomonas* and derived comparable estimates for adults (8.9 and 10.8 mL·ind.$^{-1}$·day^{-1}) and copepodites (7.0 and 8.5 mL·ind.$^{-1}$·day^{-1}) (Bogdan and Gilbert 1984; Sierszen and Frost 1990, respectively). Because grazing rates were measured using unialgal cultures, they are likely to overestimate actual grazing on natural phytoplankton assemblages (Cyr and Pace 1992). However, they provide a relative basis for comparing changes in community grazing rates by weighting abundance data on the basis of species-specific grazing rates.

Results

Phytoplankton abundance increased in response to calcite addition and fish introduction as indicated by higher chlorophyll concentrations at the treated lake relative to the reference lake (Fig. 1). Highest chlorophyll concentrations occurred during 1985, 1987, and 1990 immediately following the LT1, LT2, and WT chemical manipulations. Chlorophyll was lower during the pretreatment period (1984) and during summers when the lake exhibited partial reacidification (1986, 1988–1989, and 1991–1992). At the reference site (Dart's Lake), interannual variation in chlorophyll was small relative to that in the treated lake. Patterns of interannual variation at the two sites were not correlated, suggesting that changes in chlorophyll at the treated site were not due to the effects of annual climatic variability. We used randomized intervention analyses (RIA; Carpenter et al. 1989) to test the hypothesis that liming and fish introduction resulted in a significant change in chlorophyll concentrations at the treated lake. RIA uses paired observations from treated and reference lakes to generate a time series of between-lake differences. To test whether a nonrandom change has occurred, postmanipulation differences are compared with a reference distribution generated by random permutations of all observed differences.

The RIA procedure was run in two phases to analyze the effects of both lake and watershed chemical treatments. In the first phase (intervention = LT1), between-lake differences in chlorophyll prior to manipulation (1984) and following reacidification (1989) were compared with between-lake differences during summers when lake pH was maintained above 6.0 by directly adding calcite to the lake (1985–1988). Average between-lake differences in chlorophyll (treatment minus reference) increased from –0.579 (pH < 6.0) to +0.703 mg·m^{-3} (pH > 6.0) ($p = 0.003$). Chlorophyll concentrations at the reference lake did not exhibit pronounced trends, and therefore, we attributed the change in between-lake differences to increases in chlorophyll at the manipulated site.

In the second phase of RIA analyses (intervention = WT), between-lake differences in chlorophyll during the four summers when lake pH was maintained by direct calcite additions (1985–1988) were compared with between-lake differences during three summers following WT (1990–1992). This model tested the hypothesis that watershed application of calcite resulted in a significant change in chlorophyll relative to the period when calcite was added directly to the lake. Between-lake differences in chlorophyll (treatment minus reference) exhibited a small decrease following WT (from +0.635 to +0.251 mg·m^{-3}), but the change was not significant ($p = 0.36$). Our results suggest that the effects of the watershed calcite application were comparable with those observed in response to direct lake treatments. Hereafter, we focus on overall trends in phytoplankton and zooplankton abundance in relation to pH, irrespective of the method of treatment.

Interannual variation in chlorophyll was strongly correlated with changes in lake pH brought about by the cycle of repeated treatments and reacidification ($R^2 = 0.87$, $p = 0.0002$). Summer mean chlorophyll increased by 0.91 mg·m^{-3} (+0.13) for each unit increase in lake pH (Fig. 2). Productivity measurements (summer averages) were not significantly correlated with lake pH, but biomass-specific production (productivity per unit chlorophyll) was negatively correlated with lake pH ($R^2 = 0.71$, $p < 0.02$) (Fig. 2). Productivity per unit chlorophyll was lowest when lake chlorophyll concentrations were highest ($P:B < 1$ following LT1 and LT2) and increased after reacidification ($P:B > 2$). Estimates of brook trout abundance based on fall trap-net data varied by more than 16-fold between 1985 and 1991 due in part to high stocking rates in 1988 and 1989 (8000 and 6000 age 0+ individuals, respectively). Brook trout abundance was not a significant predictor of lake chlorophyll, primary productivity, or production per unit chlorophyll ($p > 0.05$) (Fig. 2). Log transformations of the population data did not substantially improve the regressions.

Increases in lake chlorophyll and lower biomass-specific production coincided with an overall decline in zooplankton abundance. All dominant taxa decreased in abundance after the initial lake treatment. Mean densities of *K. taurocephala* decreased from 77 491 (1984) to <100 ind.·m^{-3} (1985 and 1986). The abundance of *D. minutus* adults and copepodites decreased from 6322 (1984) to 305–960 ind.·m^{-3} (range of means for 1986–1989) (Fig. 3). *Bosmina longirostris* decreased to 33% of pretreatment densities within two summers after LT1 (Fig. 4). Mean densities of *B. longirostris* ranged from 479 to 2903 ind.·m^{-3} during 1986–1989 compared with mean densities of 8728 ind.·m^{-3} in 1984. Although daphnids were not found in samples collected prior to calcite addition, daphnids were consistently present in samples collected during 1986–1989. Of these, *Daphnia catawba* was most abundant, reaching densities of over 15 000 ind.·m^{-3} during 1986 (Fig. 4). Three other species (*D. ambigua*, *D. dubia*, and *D. parvula*) were occasionally present in samples collected during 1986–1989, although their densities were consistently low.

Because daphnids are important grazers in freshwater systems, their increased abundance during the posttreatment period could have offset the decline of small-bodied herbivorous

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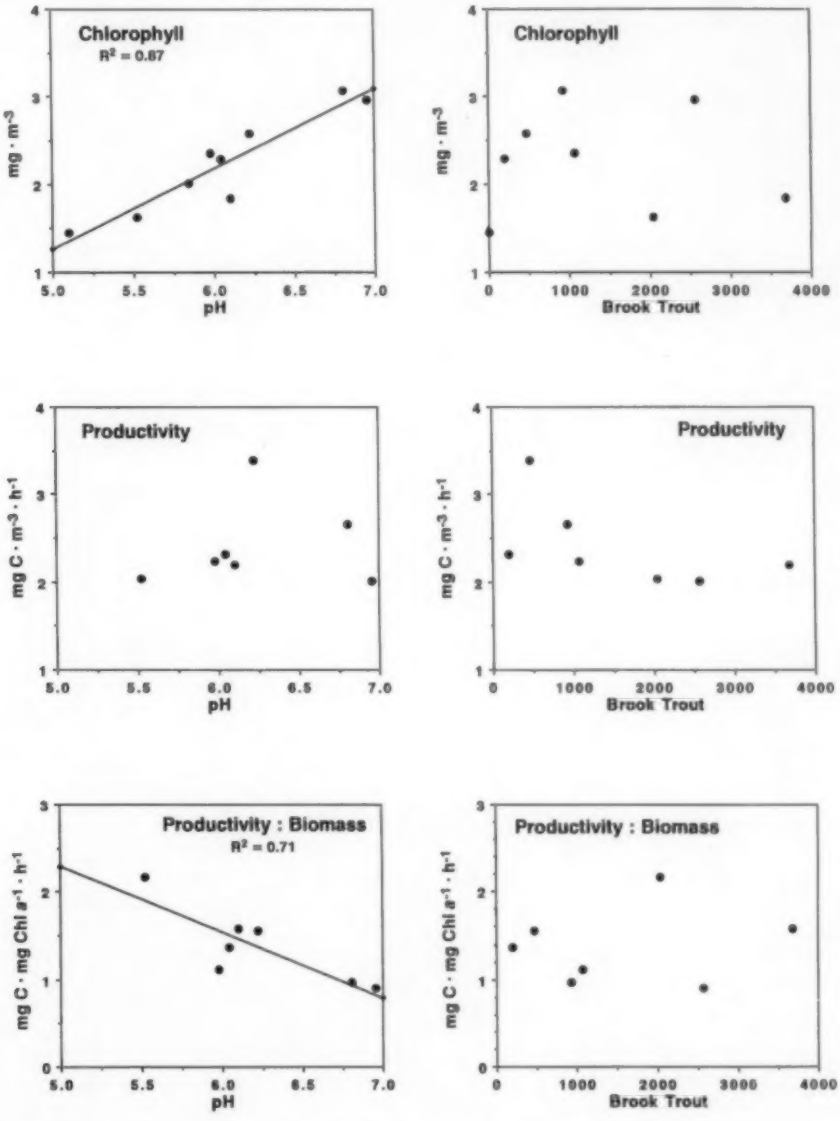
Fig. 2. Annualized estimates (summer averages) of chlorophyll, productivity, and biomass-specific production (based on chlorophyll) as a function of lake pH and brook trout abundance (lake population estimates). Regression lines are shown where a significant correlation was found ($p < 0.05$).



zooplankton. We used the species abundance data and published measurements of species-specific grazing rates to estimate community grazing (see Methods). Prior to calcite addition, estimated community grazing rates ranged from 10 to 45% of lake volume (LV) per day (Fig. 5). *Diaptomus minutus* was the most important grazer (10–35% LV·day^{-1}) due to the relatively high densities of adults and copepodites and to high individual grazing rates (8–10 mL·ind.$^{-1}$·day^{-1} for adults). *Keratella taurocephala* was also a significant contributor to community grazing (1–9% LV·day^{-1}) despite its low species-specific grazing rate (<0.5 mL·ind.$^{-1}$·day^{-1}). During the summer preceding the initial treatment, *K. taurocephala* accounted for 20% of the community grazing rate when reaching its peak midsummer density (160 000 ind.·m^{-3}). *Bosmina longirostris* was not an important grazer (0–3% LV·day^{-1}) due to low densities and its low species-specific grazing rate (1–2 mL·ind.$^{-1}$·day^{-1}).

During the posttreatment period (1985–1989), inferred community grazing rates were consistently lower with the exception of a single date in 1985 when densities of *D. minutus* and *B. longirostris* peaked after a large phytoplankton bloom. Overall, summer-averaged grazing rates declined from 34 (pretreatment) to 18% LV·day^{-1} (1985) and ranged from 2 to 8% LV·day^{-1} during 1986–1989. Reductions in grazing were

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Fig. 3. Densities of *D. minutus* adults and copepodites prior to and following calcite addition to Woods Lake. L denotes the first sampling date following the initial lake treatment (LT1).

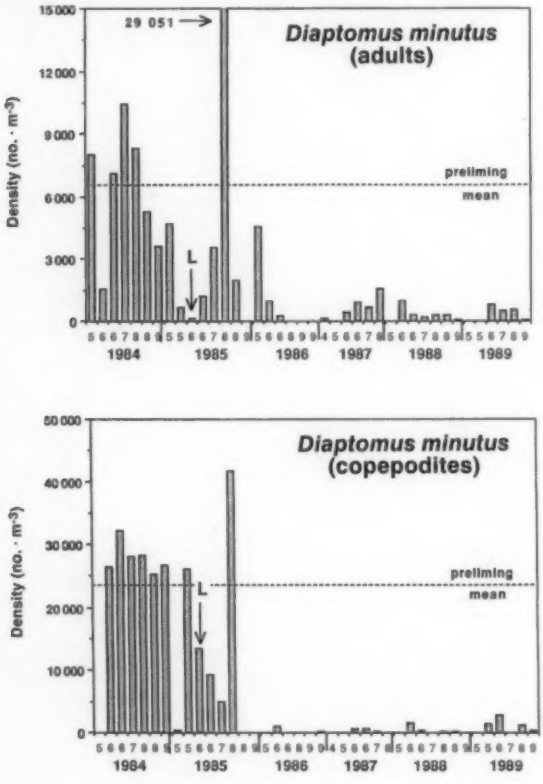
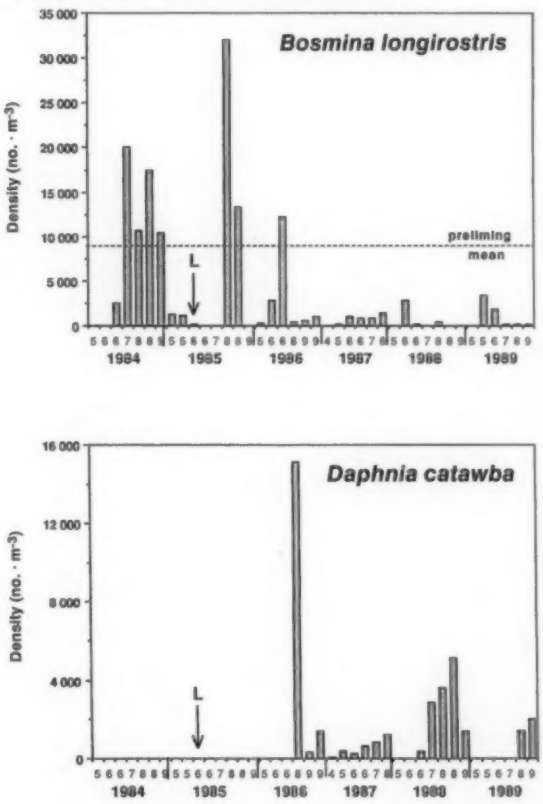


Fig. 4. Densities of *B. longirostris* and *D. catawba* prior to and following calcite addition to Woods Lake. L denotes the first sampling date following the initial lake treatment (LT1).



primarily due to the decline of the *D. minutus* population. Although daphnids were present in Woods Lake during 1986–1989, their contribution to community grazing was small due to their low densities. Despite high species-specific grazing rates (10 mL·ind.$^{-1}$·day^{-1}), *Daphnia* grazing averaged less than 5% LV·day^{-1} and maximal rates were only 16% LV·day^{-1} (in August 1986). Results from these analyses suggest that zooplankton grazing was lower after calcite addition and that the presence of daphnids was not sufficient to offset the decline of small-bodied herbivorous zooplankton.

Discussion

In this study, a concurrent chemical and biological manipulation was undertaken to assess the efficacy of liming in restoring food webs suitable for sustaining sport fish populations. Within the constraints imposed by this design, we evaluate long-term data from Woods Lake focusing on the phytoplankton–zooplankton interface. First, we compare our data with results from lake acidification experiments to address a number of issues pertaining to ecosystem stress and recovery. Specifically, we focus on whether changes in plankton community structure and function during the recovery of Woods Lake could have been predicted based on trends observed during whole-lake acidification experiments. Second, we address a number of questions specific to the restoration of anthropogenically acidified lakes.

The whole-lake experiments conducted at Little Rock Lake (LRL) in Wisconsin and at the Experimental Lakes Area (ELA) in Canada documented biotic responses during acidification from a pH of 6.1–6.8 to 4.7–5.1 (Schindler et al. 1991). Although this range of pH approximates that reported here for Woods Lake (5.1–6.9), there are important differences in the intensity and frequency of the respective chemical treatments that complicate direct comparisons. In the acidification experiments, the pH of each lake was lowered to a preselected value and then maintained for 1–2 years by repeated acid additions. This resulted in a 1.5- to 2-unit decrease in pH over 4–6 years. At Woods Lake, the first lake treatment resulted in an increase of almost 2 pH units within 48 h. Such rapid increases in lake pH may have deleterious effects on aquatic organisms. Several studies have reported significant reductions in zooplankton abundance immediately following base addition (Scheider et al. 1975; Hultberg and Andersson 1982). In Woods Lake, zooplankton densities were significantly reduced within 1 week after LT1 (Schaffner 1989). Adverse effects appeared to be short term in nature because zooplankton recovered to pretreatment densities within 1 month. Subsequent treatments (LT2 and WT) were conducted during fall, and therefore, it is not likely that these short-term effects would have influenced

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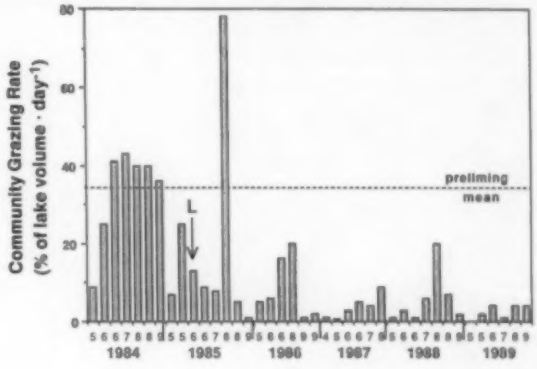
data collected during the following summer. Repeated treatments were necessary to maintain the pH of Woods Lake. This cycle of repeated additions of calcite and subsequent reacidification resulted in larger interannual variations in lake pH than those observed at LRL and ELA where acid additions were carried out weekly during the ice-free season to maintain a target pH. Despite this, the species composition of the Woods Lake zooplankton community appeared to be relatively stable during the posttreatment period. For example, we did not detect a tendency for acid-sensitive species such as daphnids to decrease in abundance during summers when the lake had partially reacidified. Nor did we observe that acid-tolerant species such as *D. minutus* attained a greater relative abundance when lake pH decreased.

Despite differences in chemical treatments, changes in species composition observed at Woods Lake were generally consistent with those reported from lake acidification experiments. Dinoflagellates and small, non-nitrogen-fixing cyanophytes increased during acidification (Schindler et al. 1991) whereas liming resulted in decreases in their relative abundance (Bukaveckas 1989; Blomqvist et al. 1994). *Keratella taurocephala* increased in abundance during acidification at LRL and ELA (Schindler et al. 1991). This species was a dominant component of the preliming community in Woods Lake but decreased following treatment. *Daphnia dubia* (LRL) and *D. galeata mendotae* (ELA) declined as pH decreased below 5.5 (Schindler et al. 1991). Daphnids did not occur in Woods Lake prior to the manipulation but were present in later years. One notable exception was the calanoid copepod *D. minutus* which decreased in abundance following the liming of Woods Lake but which also decreased during the latter stages of acidification at LRL (pH = 4.7; Brezonik et al. 1993). Because this species often dominates the zooplankton community of acidified lakes (Brett 1989), it is unclear why conditions at LRL resulted in its decline. Overall, changes in zooplankton community composition at Woods Lake were consistent with our hypothesis (hypothesis 1) that large grazers would be more abundant following the manipulation.

We had hypothesized that an increase in densities of large daphnids during the posttreatment period would result in higher community grazing rates and a corresponding increase in phytoplankton biomass turnover (hypotheses 2 and 3). In fact, we observed that phytoplankton abundance increased after calcite addition and that productivity per unit chlorophyll decreased. The strong statistical relationship between lake pH and summer-averaged chlorophyll concentrations ($R^2 > 0.80$) was striking because neither the ELA nor the LRL acidification experiments documented a correlation between pH and phytoplankton abundance (Schindler et al. 1985; Brezonik et al. 1993). We attributed increases in phytoplankton abundance and reductions in biomass turnover rates to a decrease in zooplankton grazing. Our finding that community grazing decreased after the manipulation was in contrast with those of Sierszen and Frost (1990) that grazing rates were not affected by experimental acidification of LRL.

Changes in community-level processes observed in our study but not at the experimentally acidified lakes may be an attribute of the combined chemical/biological manipulation carried out at Woods Lake. At Woods Lake, fish were not present during the pretreatment period (1984) but were reintroduced within days following LT1. At ELA (Lake 223),

Fig. 5. Inferred community grazing rates prior to and following calcite addition to Woods Lake. Grazing rates were estimated based on literature values of species-specific grazing rates. L denotes the first sampling date following the initial lake treatment (LT1).



changes in fish abundance were not evident until the second year of the experiment, and recruitment failure for all forage species did not occur until the sixth year of acidification (Schindler et al. 1985; Mills et al. 1987). Similarly, at LRL, some reduction in recruitment was noted during the first stage of acidification (years 1 and 2), but widespread recruitment failure did not occur until years 5 and 6 (Brezonik et al. 1993). We speculate that reductions in lake acidity brought about by calcite addition allowed daphnids to increase in abundance, but high rates of planktivory by stocked fish precluded them from attaining densities that would exert strong grazing pressure on phytoplankton. This hypothesis is supported by gut contents data showing that cladocerans, particularly *D. catawba*, constituted a significant proportion of prey ingested by brook trout (Gloss et al. 1989). The importance of brook trout in regulating zooplankton abundance was likely to be greatest during summer stratification when their distribution was confined to a small proportion of the water column below the thermocline and above the oxycline (Bukaveckas and Driscoll 1991*b*; Schofield et al. 1993).

The functional responses we observed (decreased zooplankton abundance and increased phytoplankton abundance) were not reported in whole-lake acidification experiments but are consistent with those observed when food webs have been manipulated to increase planktivore abundance (Carpenter et al. 1985). Increases in planktivore abundance have been shown to influence zooplankton species composition and reduce biomass which in turn may result in increased phytoplankton biomass (McQueen et al. 1986; Mills and Forney 1988; Soranno et al. 1993). We did not find, however, that brook trout abundance was a significant predictor of lake chlorophyll concentrations despite a 16-fold variation in population size. Furthermore, changes in brook trout abundance could not account for the consistent increase in chlorophyll observed during each summer following a chemical treatment. Lake chlorophyll concentrations were strongly correlated with variations in water quality imposed by the repeated pattern of calcite addition and reacidification. We cannot discount the possibility that limestone addition may have resulted in an increase in phosphorus availability and thereby stimulated phytoplankton growth rates. The effect of acidification on

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phosphorus availability has been a point of debate during the past 20 years since Grahn et al. (1974) proposed that acidification is accompanied by oligotrophication. It has been suggested that in acidic lakes, aluminum complexes with phosphorus, thereby decreasing its availability for phytoplankton uptake (Grahn et al. 1974; Broberg and Persson 1984). Aluminum may also inhibit the activity of phosphatase enzymes and thereby impede the recycling of organic phosphorus (Jansson et al. 1986). A recent review of this literature (Olsson and Pettersson 1993) has concluded that there is little experimental evidence to support the hypothesis of reduced phosphorus availability in the presence of elevated aluminum concentrations. In Woods Lake, monomeric aluminum decreased from 10 to 3 $\mu mol \cdot L^{-1}$ within 6–8 weeks following calcite addition (Driscoll et al. 1989*a*, 1996), but we did not detect any significant change in lake phosphorus concentrations during the first 3 years of the experiment (1984–1986; T. Young and J. DePinto, personal communication). Trace amounts of phosphorus contained in limestone did not contribute significantly to the lake phosphorus budget. In batch tests, the addition of limestone to Woods Lake water resulted in only a small increase in total dissolved phosphorus (0.017 $\mu g\ P \cdot mg\ CaCO_3\ added^{-1}$). Based on this estimate, we inferred that the phosphorus added during LT1 was <0.5 $\mu g\ P \cdot L^{-1}$ (ambient concentrations in Woods Lake were 5–15 $\mu g\ P \cdot L^{-1}$). A comparison of our findings with other liming studies does not reveal any consistent patterns, as both increases (Hornstrom et al. 1993) and decreases (Molot et al. 1990; Blomqvist et al. 1993) in phosphorus concentrations after calcite addition have been reported.

It is important to recognize that lake liming and acidification experiments may not provide a direct test of the oligotrophication hypothesis because both approaches consider only in-lake processes that regulate phosphorus availability. In this respect, comparing lake liming with watershed liming may provide insights as to the importance of soil processes in regulating phosphorus availability in acidic lakes. Studies of Lake Gardsjon, an acidic lake in Sweden, have shown that transport of phosphorus from the drainage basin into the lake decreased as the soil profile acidified (Jansson et al. 1986). The decrease in export was attributed to complexation of phosphorus by aluminum in the B-horizon of the soil. Results from a catchment liming experiment in Scotland indicated that monomeric aluminum concentrations in stream water decreased by 60–80% after calcite application (Grieve 1990). At Woods Lake, decreases in monomeric aluminum concentrations were observed in stream water, lake water, and soil water samples collected following WT (Cirmo and Driscoll 1996; Driscoll et al. 1996; Geary and Driscoll 1996). We hypothesized that reductions in the leaching of monomeric aluminum would result in greater phosphorus export to the lake. A comparison of chlorophyll concentrations during the period when calcite was added directly to the lake (1985–1989) with similar data collected after WT (1990–1992) did not reveal any significant differences (RIA analyses). Thus, our data do not support the hypothesis that watershed liming promoted phosphorus export from the catchment in sufficient quantities to stimulate phytoplankton production. Although a significant fraction (50%) of the added calcite dissolved within 2 years following the watershed treatment (Blette and Newton 1996), Ca^{2+} was largely retained in upper soil layers. As a result, increases in soil water pH during the first year were not sustained in subsequent years (Geary and Driscoll 1996). Continued dissolution of the limestone may over time increase the pH of soil water in the mineral horizon and result in greater phosphorus export from the catchment, but this effect was not observed during the 3-year period of this study.

Results from this and other liming studies suggest that calcite addition reverses the trend toward simplification of food webs commonly observed in anthropogenically acidified lakes. Increases in the relative abundance of acid-sensitive species of phytoplankton and zooplankton suggest that recovery can be relatively rapid once water quality conditions improve. Liming also permitted the reintroduction of a native fish species (brook trout), and catchment liming improved their spawning success by allowing them to utilize tributary streams (Schofield and Keleher 1996). Other trophic groups not considered in this paper showed similar responses. For example, vegetation surveys showed that the aquatic plant community in Woods Lake had gained seven new species within 6 years after liming (Weiher et al. 1994). Improved water quality benefited a wide range of acid-sensitive species, but the implications for ecosystem functioning are more difficult to discern, in part because the combined chemical and biological manipulation precludes a rigorous analysis of top-down and bottom-up mechanisms. Although we correctly predicted qualitative shifts in zooplankton community composition, we underestimated the importance of planktivory by brook trout in regulating the abundance of daphnids. Unexpected changes in habitat suitability may have fostered the dependence of brook trout on zooplankton prey. These included the reduction in light penetration and associated decline of littoral macrophyte beds (Bukaveckas 1988) and changes in thermal stratification which were accompanied by increased hypolimnetic oxygen depletion (Bukaveckas and Driscoll 1991*b*; Schofield et al. 1993). Other studies have also documented the plasticity of this species in switching from benthic to planktonic feeding habits (Tremblay and Magnan 1991). Our experience is similar to others involved in whole-lake experiments in that indirect pathways were found to give rise to unexpected behavior of "pivotal" species (sensu Carpenter et al. 1993) which was manifested at the ecosystem level.

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Fatty acid signatures and classification trees: new tools for investigating the foraging ecology of seals

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Abstract: Analysis of the fatty acid composition of milk lipids in marine mammals offers a potential means of determining changes in diet and lactation stage. However, the large number of fatty acids routinely identified (over 60) relative to the number of animals usually sampled can limit the usefulness of standard multivariate statistical models for characterizing these patterns. Classification trees or tree-based models, which are not limited by the number of variables, were used here to study the fatty acid patterns in the milk of female harbour seals (*Phoca vitulina*) at parturition and during lactation. Tree analyses correctly classified 44 of 51 seals based on milk fatty acid composition to four stages of lactation, which corresponded to states of fasting versus increasingly intensive feeding. The fatty acid 16:2*n*–6 was quite effective in differentiating between seals at parturition and those 4 days or more later. Seals were grouped into early and late lactation by fatty acid 24:1*n*–9. A comparison between classification rules derived from classification trees and discriminant analysis showed that each gave similar rates of misclassification but that the latter required a method for the a priori choice of which fatty acids to analyze.

Résumé : L'analyse de la composition en acides gras des lipides du lait chez les mammifères marins constitue une méthode possible pour déterminer les changements dans le régime alimentaire et le stade de lactation. Cependant, le grand nombre d'acides gras (plus de 60) identifiés de manière habituelle par rapport au nombre d'animaux habituellement échantillonnés peut limiter l'utilité des modèles statistiques standard à variables multiples pour la caractérisation de ces compositions. Des arbres de classification ou des modèles arborescents, qui ne sont pas limités par le nombre de variables, ont été utilisés pour étudier les profils d'acides aminés dans le lait de phoques communs (*Phoca vitulina*) femelles au moment de la parturition et de la lactation. Les analyses par arborescence ont permis de classer correctement 44 des 51 phoques à partir de la composition du lait en acides gras pour quatre étages de lactation, qui correspondaient à des états de jeûne par opposition à des périodes d'alimentation de plus en plus intensives. L'acide gras 16:2*n*–6 était relativement efficace pour distinguer les phoques à la parturition des phoques qui en sont rendus à quatre jours ou plus après la parturition. Les phoques ont été regroupés en deux groupes (début et fin de la lactation) par l'acide gras 24:1*n*–9. Une comparaison entre les règles de classification dérivées des arbres de classification et de l'analyse de discrimination a révélé que chacune de ces méthodes donnaient des taux semblables d'erreurs de classification, mais que la dernière exige une méthode pour choisir a priori les acides aminés à analyser.
[Traduit par la Rédaction]

Introduction

It has been recognized for some time that dietary fatty acids affected the fatty acid composition of the blubber lipids of baleen whales and phocid seals (e.g., Klem 1935; Ackman and Eaton 1966; Ackman et al. 1971). Building on these early observations, Iverson (1988, 1993) proposed that the pattern of fatty acids ("fatty acid signatures") in the blubber and milk of marine mammals might be used to determine changes in and the components of their diets. A recent study of the transfer of milk fatty acids from hooded seal (*Cystophora cristata*) mothers to their pups illustrates this approach (Iverson et al. 1995*a*). In this study, the female's milk was the "prey" and the pup the "predator". Milk fatty acid signatures can also be useful in studies of the foraging ecology of terrestrial carnivores, such as the black bear (*Ursus americanus*) (Iverson and Oftedal 1992).

Lipids in marine organisms are characterized by their great diversity and high levels of long-chain and polyunsaturated fatty acids that originate in various unicellular phytoplankton and seaweeds (Ackman 1980). Fatty acids are the most abundant constituent of common lipids. Unlike other nutrients, such as proteins and carbohydrates which are readily broken down during digestion, in monogastric animals, dietary fatty acids pass into the circulation intact and those of carbon chain length >14 can be deposited in animal tissue with little or no modification. Thus, it is possible to consider the pattern of fatty acids in the blubber of a pinniped as a signature that should reflect an integration of the fatty acid signatures of the major prey items in the diet (Iverson 1993).

The diversity of marine fatty acids (over 60 can be routinely identified) presents a problem for their statistical analysis. In most multivariate methods used (e.g., discriminant analysis, principal component analysis) to characterize patterns in the fatty acids and identify groups of prey, or the nutritional state of the animals, the number of animals sampled must exceed the number of variables. With over 60 variables, this puts a

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considerable burden on investigators to obtain extremely large numbers of samples. One approach to this problem has been to select a subset of major fatty acids (usually about 12–18) for multivariate analysis (e.g., Grahl-Nielsen and Mjaavatten 1991). The disadvantages of this approach are that fatty acid selection is subjective and information may be lost in the process. Others have attempted to avoid this problem by using univariate methods, but the probability of type 1 error increases rapidly given the large number of comparisons that must be made.

In contrast with these multivariate methods, classification trees or tree-based models (Breiman et al. 1984; Clark and Pregibon 1992) offer a means of characterizing patterns and identifying groups with as many fatty acids as available, even if this number exceeds the number of animals sampled. This method proceeds by recursively partitioning the subjects into two or more groups based on a series of dichotomous splits from a set of explanatory variables — fatty acids in this case. The entire set of fatty acids can be screened by this procedure to choose a subset that can be used to classify subjects into relatively homogeneous groups based on similarities in patterns of fatty acid proportions. The tree-based models are unaffected by spurious correlations, do not require a statistical distribution assumption for the observations, use computer power to test all of the fatty acids, and use a statistical criterion (change in deviance which is directly related to the log-likelihood) to choose a subset of fatty acids. In addition, the visual nature of the trees makes them easy to present and understand.

The harbour seal (*Phoca vitulina*), a member of the family Phocidae, is found in coastal marine habitats throughout the Northern Hemisphere. Pregnant harbour seal females haul out on Sable Island and give birth between mid-May and June after a period of intensive fattening in preparation for lactation. In contrast with other phocid species, the small body size of adult female harbour seals apparently precludes their ability to support all of lactation from stored energy (Bowen et al. 1992). Recent studies using time–depth recorders have shown that, after about 6 days postpartum, most females exhibit intermittent foraging bouts, which after about 11 days become increasingly intensive in both depth and duration as lactation progresses (Boness et al. 1994).

We collected milk samples from adult females at parturition and over the course of lactation and used the analysis of fatty acid signatures to investigate their foraging ecology. We hypothesized that milk samples taken at parturition and during initial fasting should reflect blubber stores and hence represent an integrated view of the diet prior to giving birth whereas samples taken after the onset of feeding trips should reflect current feeding (e.g., Iverson 1993; Iverson et al. 1995*a*, 1995*b*, 1997). However, the purpose of this paper is not to explicitly examine the foraging ecology of these females, but to illustrate the use of classification trees in the analysis of milk fatty acids, which together offer some promise as useful tools in such studies.

Methods

Milk samples were collected from female harbour seals during the May–June pupping seasons in 1990 and 1993 on Sable Island, Nova Scotia, Canada (43°55′N, 60°00′W). Each day, all newly born pups were individually tagged in the hind flipper such that the age of pups and hence stage of lactation of the females was known to within 24 h.

In 1990, females were captured on the day of parturition (Day 0) and at 4–7, 12–14, and 19–21 days postpartum. In 1993, females were captured on the day of parturition and 19–21 days postpartum. At each capture, females were sedated with valium (0.2 mg/kg body mass, intravenous injection into the extradural vein) and milked using syringe suction (Iverson et al. 1993). To facilitate milking, females were given an intramuscular injection of oxytocin (15–30 IU). Approximately 60-mL samples were obtained from each female. At the time of collection, a 0.5-mL aliquot of milk was placed in a Kimax tube containing 3 mL of 2:1 (v/v) chloroform–methanol containing 0.01% BHT (w/v) and stored frozen.

Fatty acid analyses

Lipids were extracted into chloroform according to the method of Folch et al. (1957) as modified by Iverson (1988) using the ratios of 18 parts 2:1 chloroform–methanol to 1 part sample and 3 parts solvent to 1 part aqueous salt (i.e., milk plus 0.7% NaCl). Fatty acid methyl esters were prepared from 100 mg of the pure extracted lipid (filtered and dried over anhydrous sodium sulfate) using 1.5 mL of 8% boron trifluoride in methanol (v/v) and 1.5 mL of hexane, capped under nitrogen, and heated at 100°C for 1 h. Fatty acid methyl esters were extracted into hexane, concentrated, and brought up to volume (50 mg/mL) with high-purity hexane. This method produced results identical to those using 0.5 N H_2SO_4 in methanol as transesterfying reagent.

Duplicate analyses of fatty acid methyl esters and their identifications were performed using temperature-programmed gas–liquid chromatography basically according to Iverson (1988) and Iverson et al. (1995*a*) on a Perkin Elmer Autosystem II Capillary FID gas chromatograph fitted with a 30-m column (0.25-mm inside diameter) coated with 50% cyanopropyl polysiloxane (0.25-μm film thickness; J&W DB-23; Folsom, Calif.) and linked to a computerized integration system (Turbochrom 4.0 software, PE Nelson). Individual fatty acids are expressed as mass percentage of total fatty acids and designated by shorthand IUPAC nomenclature of carbon chain length:number of double bonds, and location (n–x) of the double bond nearest the terminal methyl group. For example, a fatty acid with a carbon chain length of 16, one double bond, and the location of this double bond 7 carbons back from the terminal methyl group would be designated as 16:1n–7.

Classification and regression tree analysis

A total of 51 milk samples were collected from females sampled in 1990. These samples were classified into four categories based on the days postpartum when they were collected: 0 days (n = 15), 4–7 days (n = 15), 12–14 days (n = 12), and 19–21 days (n = 9). We called this our "training sample". We wanted to be able to predict which of these four categories a seal belonged to based only on the fatty acid composition of the milk sample from the animal.

Next, each of our predictor variables (i.e., fatty acids) was screened by the classification tree algorithm (see below) to see which would best classify observations into a particular category. For example, the proportion of one particular fatty acid in the milk might separate the majority of the seals in the first two day-categories from those in the latter two day-categories. Additionally, another fatty acid might be instrumental in separating seals in the Day 0 group from those in the Days 4–7 group whereas a different fatty acid may separate seals in the Days 12–14 and 19–21 categories. Thus, the procedure is best described as creating an inverted tree structure with the root node at the top and with the original observations represented as vector y_0 = (15,15,12,9), where each position represents its respective day-category. For a specified fatty acid, observations in this vector will be classified as "travelling" down either the left branch or right branch leading away from the root node to other intermediate nodes. The decision on whether a particular seal is assigned to the right branch or

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Table 1. Fatty acids in harbour seal milk samples from Sable Island, Nova Scotia (1990).

	Day-category			
Fatty acid	0 (n = 15)	4–7 (n = 15)	12–14 (n = 12)	19–21 (n = 9)
12:0	0.17	0.17	0.21	0.21
13:0	0.00	0.00	0.00	0.00
14:0	4.57	4.28	3.95	3.48
14:1*n*–9	0.17	0.17	0.20	0.20
14:1*n*–7	0.04	0.02	0.01	0.03
14:1*n*–5	0.32	0.43	0.45	0.55
Iso 15	0.24	0.18	0.23	0.21
Anti 15	0.20	0.12	0.14	0.13
15:0	0.38	0.36	0.35	0.31
15:1	0.02	0.01	0.01	0.03
Iso 16	0.18	0.11	0.10	0.11
16:0	15.65	14.43	13.06	11.92
16:1*n*–11	0.61	0.61	0.59	0.60
16:1*n*–9	0.45	0.39	0.39	0.44
16:1*n*–7	9.69	10.53	9.56	9.41
7Me16:0	0.34	0.31	0.28	0.24
16:1*n*–5	0.33	0.30	0.36	0.32
16:2*n*–6	0.14	0.10	0.06	0.07
16:2*n*–4	0.36	0.39	0.45	0.44
16:3*n*–6	0.47	0.45	0.38	0.31
16:3*n*–4	0.29	0.27	0.23	0.19
16:3*n*–1	0.22	0.19	0.21	0.21
16:4*n*–1	0.57	0.58	0.43	0.31
17:0	0.23	0.22	0.24	0.25
17:1	0.34	0.36	0.38	0.42
18:0	2.50	2.22	2.40	2.34
18:1*n*–13	0.06	0.05	0.03	0.00
18:1*n*–11	3.37	2.97	3.04	3.89
18:1*n*–9	13.49	13.71	14.56	16.94
18:1*n*–7	4.11	3.87	3.76	3.78
18:1*n*–5	0.71	0.64	0.62	0.57
18:2Δ5.7	0.25	0.22	0.21	0.25
18:2*n*–7	0.08	0.04	0.02	0.01
18:2*n*–6	1.36	1.35	1.48	1.62
18:2*n*–4	0.28	0.22	0.18	0.15
18:3*n*–6	0.26	0.20	0.20	0.20
18:3*n*–4	0.23	0.18	0.16	0.16
18:3*n*–3	0.47	0.58	0.67	0.72
18:3*n*–1	0.06	0.04	0.03	0.03
18:4*n*–3	1.33	1.39	1.40	1.23
18:4*n*–1	0.45	0.34	0.25	0.20
20:1*n*–11	1.21	1.24	1.38	1.72
20:1*n*–9	3.90	4.77	5.52	6.34
20:1*n*–7	0.34	0.34	0.44	0.46
20:1*n*–5	0.06	0.08	0.09	0.12
20:2*n*–9	0.02	0.03	0.02	0.00
20:2*n*–6	0.22	0.21	0.25	0.24
20:3NMIT	0.01	0.02	0.02	0.02
20:3*n*–6	0.09	0.05	0.05	0.06
20:4*n*–6	0.66	0.64	0.60	0.54
20:3*n*–3	0.04	0.06	0.08	0.08
20:4*n*–3	0.57	0.57	0.64	0.62
20:5*n*–3	9.95	8.56	7.30	5.97
21:5*n*–3	0.54	0.52	0.66	0.42
22:1*n*–11	1.32	1.48	2.06	2.01
22:1*n*–9	0.31	0.32	0.44	0.51
22:1*n*–7	0.01	0.00	0.03	0.02
22:2*n*–6	0.10	0.11	0.12	0.16
22:4*n*–6	0.07	0.07	0.09	0.08
22:5*n*–6	0.12	0.14	0.18	0.22
22:4*n*–3	0.07	0.10	0.10	0.14
22:5*n*–3	4.52	4.68	4.75	4.83
22:6*n*–3	10.27	12.40	13.11	12.08
24:1*n*–11	0.18	0.18	0.22	0.23
24:1*n*–9	0.22	0.21	0.32	0.33

Note: Mean percentage composition by mass for each fatty acid according to day-category. Sample size (n) is given for each category.

Table 2. Results from setting the first node of the classification tree in different ways: (*a*) standard method of choosing explanatory variable (e.g., fatty acid) that gives the maximum change in deviance and (*b*–*d*) deliberately setting the first node to fatty acid 16:0, 7Me16:0, or 18:3*n*–4, respectively.

	No. of terminal nodes	Residual mean deviance	Misclassification error rate	Variables used in tree construction
(*a*)	8	0.6504	7/51	16:2*n*–6, 24:1*n*–9, 17:1, 16:3*n*–6, 18:2Δ5,7, 12:0, 16:0
(*b*)	8	0.6346	7/51	16:0[a], 18:2*n*–6, 16:3*n*–6, 18:2Δ5,7, 16:2*n*–6, 20:3*n*–6
(*c*)	7	0.7176	7/51	7Me16:0, 16:3*n*–6, 16:1*n*–7, 16:2*n*–6, 16:0, 14:1*n*–5
(*d*)	6	0.7907	8/51	18:3*n*–4, 7Me16:0, 16:3*n*–6, 12:0, 16:2*n*–6

[a]Used in two different locations on tree.

left branch will depend on whether the observed level for the specified fatty acid is above or below some cutoff value. At each of the intermediate nodes, another fatty acid is used to assign observations to even more left and right branches until a terminal node is reached. Ideally, a terminal node will have observations belonging to one group only, e.g., $y_k = (15,0,0,0)$. The decisions and branches taken to get to this node will define, in this case, seals in the Day 0 category.

Which predictor variable (fatty acid) and what cutoff value is used is determined for each node by calculating the maximum change in deviance:

(1) $D(\mu; y) - D(\hat{\mu}_L, \hat{\mu}_R; y)$.

The term on the left corresponds to the deviance at the root node and the term on the right is the sum of the deviances for the left ($\hat{\mu}_L$) and right branches ($\hat{\mu}_R$) or splits. The deviance function is defined as minus twice the log-likelihood function (Clark and Pregibon 1992):

$$D(\mu; y) = -2 \sum_{i=1}^{n'} \sum_{k=1}^{K} y_{ik} \log (p_{ik});$$

K groups, n' observations in the node.

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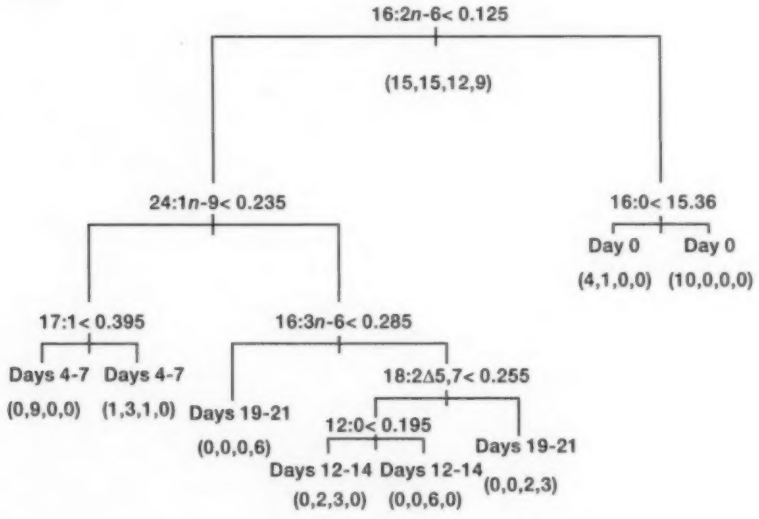
Fig. 1. Initial classification tree for determining days postpartum from fatty acids measured in harbour seal milk samples collected in 1990. The length of descending branches is proportional to change in deviance (see text). The fatty acid and the cutpoint are given for each node in the tree, with the less than sign referring to the left-hand decision. The right-hand decision was made for all values of the fatty acid greater than or equal to the cutpoint. Entries under the first node refer to the original number of seals in each of the four categories (Day 0, Days 4–7, Days 12–14, Days 19–21). Entries under each of the terminal nodes refer to the original categories of the seals assigned to the category given as the name of the terminal node.



We used the tree functions in S-PLUS (version 3.3 for Windows (1995), Statsci Division, MathSoft Inc., Seattle, Wash.) to conduct our analysis (see also Venables and Ripley 1994). The default criteria in S-PLUS for terminating branching are a change in deviance of <1% of the root node deviance or when the minimum number of observations at a node was <10. These stopping rules tend to be conservative and thus, "pruning" back of the tree is often necessary (see Results) to prevent overfitting of variables. The stopping rules used here are not the only ones being used and alternatives are discussed in Breiman et al. (1984) and Venables and Ripley (1994).

Misclassification rates for the final tree are generally calculated by predicting the categories for the same data that were used to construct the tree. Such estimates, referred to as resubstitution error rates, usually underestimate the true error rate. Therefore, we also used the k-fold cross-validation and leave-one-out methods. Misclassification rates using k-fold cross-validation are estimated by dividing the n observations randomly into k roughly equal-sized groups and using the data from $k - 1$ of the groups to construct the tree. This tree is then used to predict the categories for the one group of data held back. In the related leave-one-out method, the tree is constructed with $n - 1$ observations and used to predict the category of the one observation that was held back. The difference between the two methods is that the cross-validation estimate is usually applied to one random realization of k groups whereas the leave-one-out method constructs n trees leaving each observation out in turn.

Results

In all of the 1990 samples, 50 of the 65 milk fatty acids quantified each accounted for <1% by mass of the total fatty acids in the milk (Table 1). The dominant fatty acids (>2%) were 14:0, 16:0, 16:1*n*–7, 18:0, 18:1*n*–11, 18:1*n*–9, 18:1*n*–7, 20:1*n*–9, 20:5*n*–3, 22:1*n*–11, 22:5*n*–3, and 22:6*n*–3. These 12 fatty acids in total accounted for 83.3, 84.0, 83.1, and 83.0%, respectively, of the total fatty acids for all four day-categories.

Classification of the milk samples from 1990 into their day-categories required seven fatty acids, resulting in eight terminal nodes on the tree (Fig. 1). The residual mean deviance for this tree was 0.6504. Fatty acid 16:2*n*–6 was chosen by the tree algorithm for the first node based on maximum change in deviance (47.096). All milks with proportions of 16:2*n*–6 ≥0.125% were eventually classified as Day 0 categories. Fatty acid 16:0 was selected to differentiate between the 14 Day 0 milks and the one Days 4–7 sample that were directed down the right branch from the root node. On the main left branch of the tree, 24:1*n*–9 separated Days 4–7 samples from Days 12–14 and 19–21 samples. Fatty acid 17:1 was chosen to break out the one misclassified Day 0 and three Days 12–14 samples. Finally, three fatty acids, 16:3*n*–6, 18:2Δ5,7, and 12:0, were used to further separate the remaining Days 12–14 and 19–21 samples. This initial tree misclassified 7 out of the 51 cases.

The choices of cutpoints for the fatty acids used to construct the tree in Fig. 1 are illustrated in Fig. 2. The boxplots in the panels of this figure summarize the distributions of the observed proportions by day-category for each of the fatty acids used to construct the tree. In the top left panel the distribution of fatty acid 16:2*n*–6 for all 51 cases is given. The cutpoint of 0.125 was best for differentiating between the Day 0 samples and the rest of the day-categories with the minimal amount of misclassification. The middle top panel presents the distribution for fatty acid 24:1*n*–9 for those samples not assigned to the right branch and eventually classed as Day 0 (top right panel). Terminal nodes are named according to which of the categories assigned to the node were the most abundant. Similarly, the rest of the panels present the distributions only for those samples that were remaining to be tested for that specific fatty acid. With the exception of 16:0, the fatty acids used to

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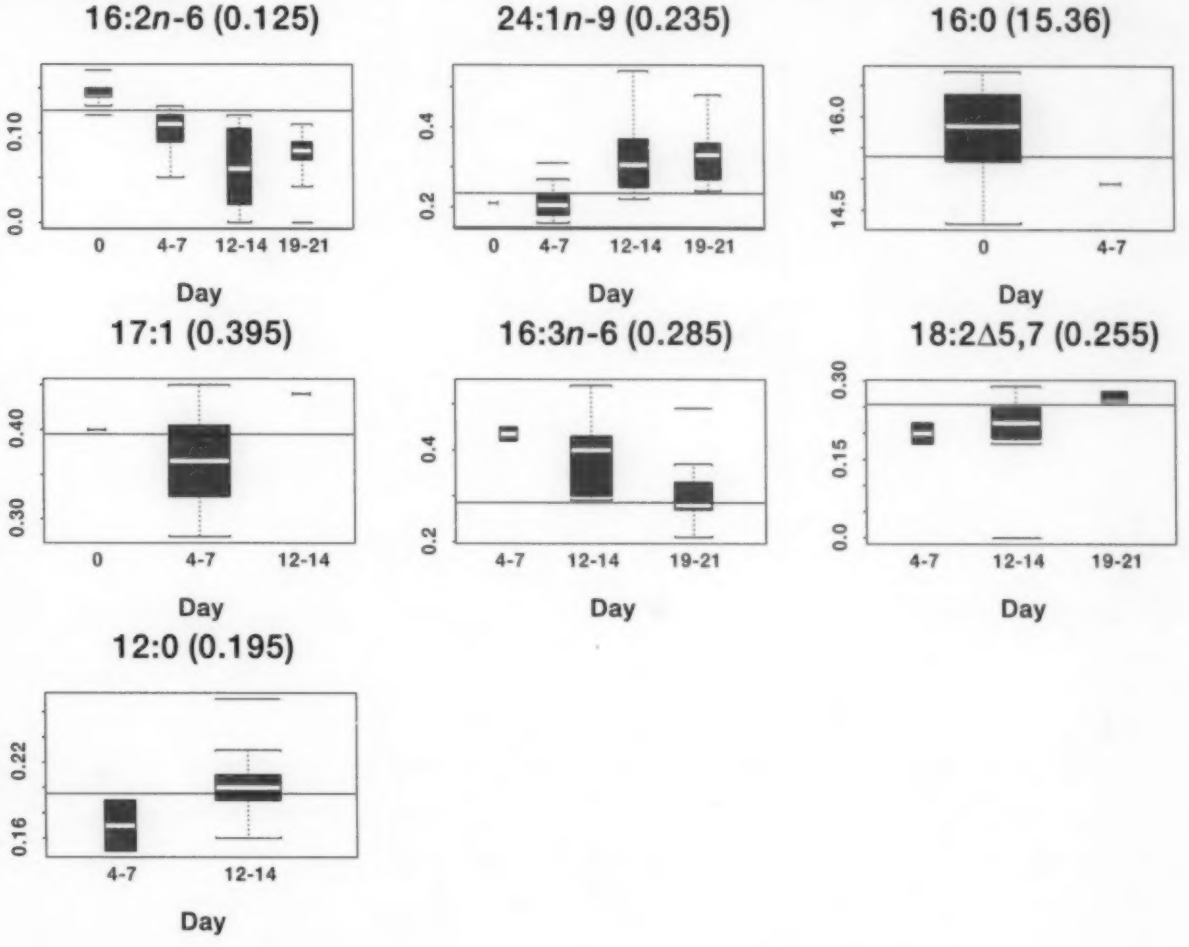
Fig. 2. Boxplots demonstrating how the cutpoints (full horizontal lines) were used to classify the seals according to the different categories of days postpartum for each of the fatty acids used in the initial tree plot in Fig. 1. The positions of the medians are represented as white horizontal bars within a box, and the upper and lower boundaries of the box indicate the upper (75th) and lower (25th) quartiles, respectively. Vertical lines from the boxes extend to 1.5 times the interquartile range or to the closest observed value. Disconnected horizontal lines are used to indicate extreme values.



construct the tree were minor components (<1%) of the total mass of all of the fatty acids.

The changes in deviance for all of the fatty acids as root node contenders are presented in Fig. 3. Whereas 16:2*n*–6 gave the largest change, three other fatty acids, 16:0, 7Me16:0, and 18:3*n*–4, also resulted in changes of deviance in excess of 40. Using any one of these three fatty acids at the root node resulted in similar classification and misclassification rates (Table 2).

The tree using 16:0 at the root node is the closest to the original tree (Fig. 1), having the same misclassification rate and a slightly lower residual mean deviance. Whereas the residual mean deviance reflects the goodness of fit of the whole tree, the trees are constructed one node at a time. Therefore, it is likely that the tree constructed recursively by having the largest change in deviance at each node will not explain the largest amount of deviance overall. However, the difference in residual mean deviance between the original tree and that with 16:0 as the first node is quite small and there is no theory yet to statistically test the difference in deviance between the two trees. The difference of 0.0158 is well within the 1% change used for the stopping rules. In comparing misclassification rates, the two trees are equivalent.

The stopping rules used to construct the initial tree were largely arbitrary, but commonly used, and may have resulted in overfitting of variables. Starting with the tree in Fig. 1, fatty acids were successively removed or "pruned" and both the residual mean deviance and the misclassification rate of the resultant tree were calculated. From our point of view, misclassification rate is a more important criterion than change in deviance for judging alternative pruned trees (Fig. 4). The error rate of 7/51 remained constant for trees with five, six, seven, and eight nodes and then increased for fewer nodes than these (Fig. 4, left panel). The "best" five-node tree (Fig. 4,

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Fig. 3. Dot chart of the change in deviance for the optimal cutpoint for each of the fatty acids used in this study to determine the fatty acid used for the first node. Fatty acid 16:2*n*–6 had the largest change at 47.096 (upper left panel) and thus was algorithmically chosen for the first node in Fig. 1.

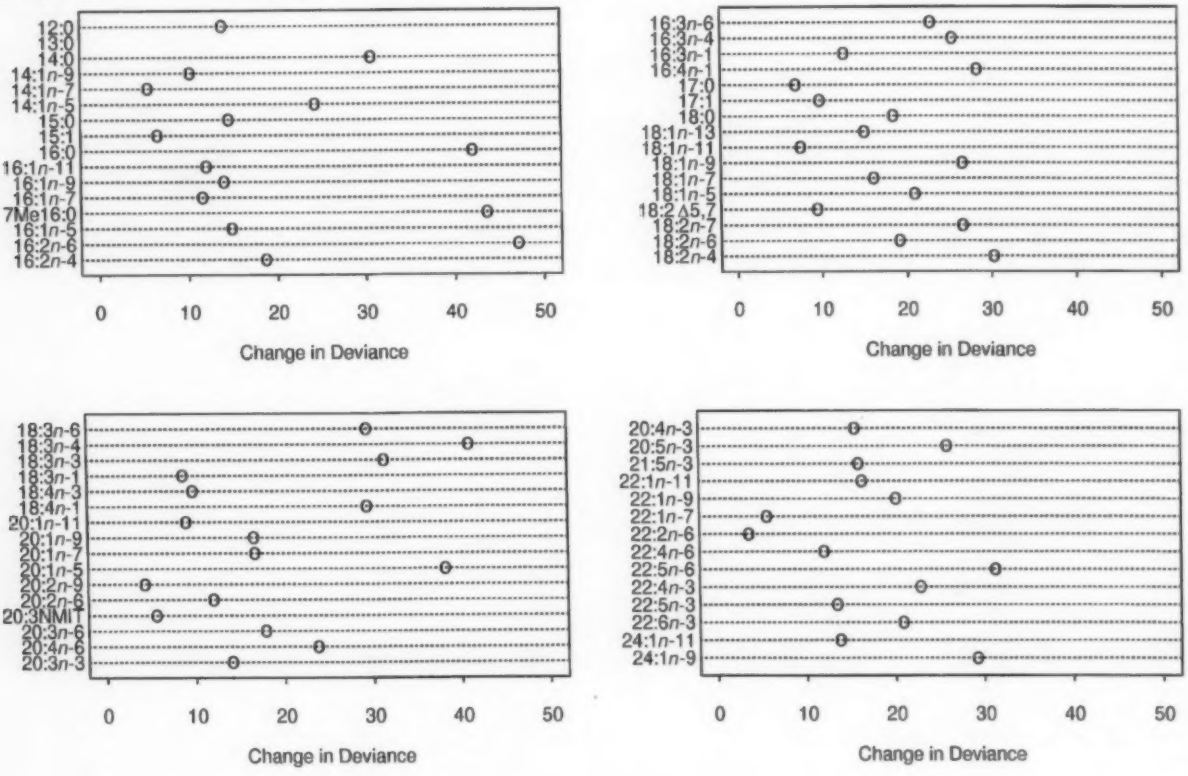

Table 3. Prediction results from applying the pruned tree from the 1990 data to the harbour seal sample collected in 1993.

			Fatty acids used in pruned tree			
Case No.	Observed	Predicted	16:2*n*–6 0.125	24:1*n*–9 0.235	16:3*n*–6 0.285	18:2Δ5,7 0.255
1	Days 19–21	Days 12–14	0.11	0.26	0.37	0.20
2	Days 19–21	Days 12–14	0.11	0.49	0.68	0.14
3	Days 19–21	Days 12–14	0.11	0.45	0.55	0.18
4	Days 19–21	Days 4–7	0.09	0.07	0.38	0.14
5	Days 19–21	Days 12–14	0.12	0.28	0.37	0.19
6	Day 0	Day 0	0.18	0.19	0.46	0.41
7	Day 0	Day 0	0.19	0.21	0.37	0.31
8	Day 0	Day 0	0.18	0.2	0.48	0.26
9	Day 0	Day 0	0.17	0.17	0.46	0.24
10	Day 0	Day 0	0.24	0.18	0.60	0.32
11	Day 0	Day 0	0.15	0.15	0.47	0.21
12	Day 0	Day 0	0.21	0.2	0.46	0.31
13	Day 0	Day 0	0.15	0.16	0.42	0.24
14	Day 0	Day 0	0.19	0.21	0.54	0.27
15	Day 0	Day 0	0.15	0.11	0.43	0.23

right panel) required only four fatty acids to discriminate between the four day-categories. The mean residual deviance of this tree was 0.8427. Dropping 17:1, 12:0, and 16:0 from the original tree is easily understood when misclassification rates are considered. For example, 16:0 was used to separate the one Days 4–7 sample from the 14 Day 0 samples classified to the right branch from the first node. However, because node names reflect the major category assigned, the Days 4–7 sample was

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Fig. 4. Results of pruning the tree in Fig. 1 by the number misclassified criterion. The left panel gives the number misclassified as a function of the number of terminal nodes in the tree. The right panel presents the optimal pruned tree, which has the same misclassification rate as the original tree but with only five terminal nodes instead of the eight in the original tree. Labeling of the tree as per Fig. 1.

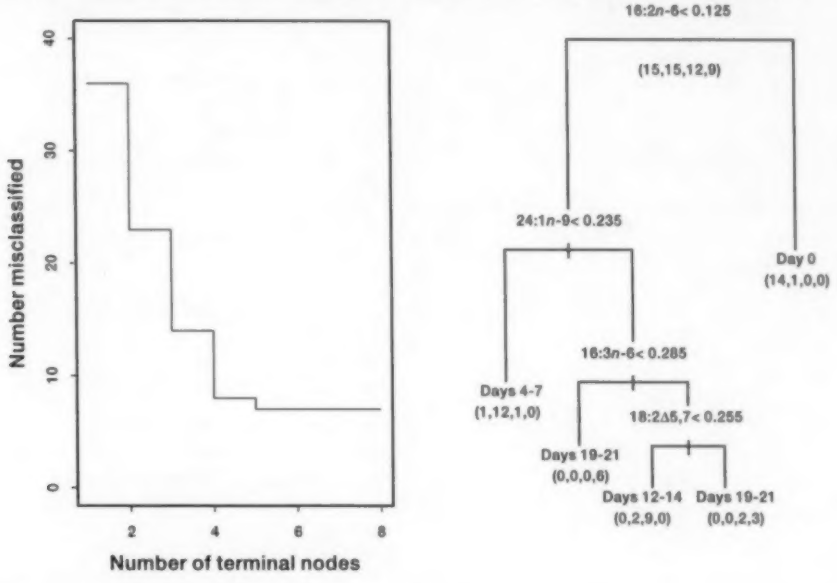
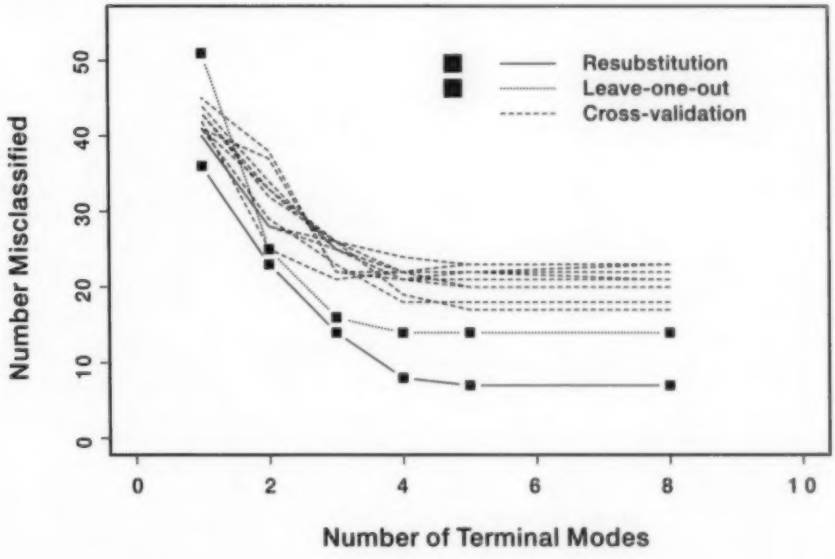


Fig. 5. Comparison of misclassification rates estimated for different-sized optimal pruned trees by the methods of resubstitution, leave-one-out, and 10-fold cross-validation.



still misclassified. Thus, these pruned fatty acids did not reduce the misclassification error rate and therefore were superfluous.

Misclassification rates estimated from cross-validation and leave-one-out methods were compared with resubstitution rates for a series of pruned trees in Fig. 5. The cross-validation rates represent 10 random realizations for the data divided into 10 groups. For the five-node tree, the leave-one-out estimate of 14/51 (0.275) misclassified is twice the resubstitution rate of 7/51 (0.137). However, the cross-validation rates range from 16 to 27 misclassified out of 51 (0.314–0.529).

All of these misclassification rates are meant to evaluate the future performance of the tree on a sample independent of that used to construct the tree. We applied the pruned tree given in Fig. 4 to fatty acid observations from 15 lactating harbour seals sampled on Sable Island in 1993. The misclassification rate

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Table 4. Discriminant analysis results for three methods of choosing variables (fatty acids) to be included: (*a*) subset of fatty acids used by Grahl-Nielsen and Mjaavatten (1991) (stepwise discriminant analysis using Wilks Λ criterion for entering and removing variables; proportion of total variation explained by each discriminant axis = 0.87, 0.12, 0.01), (*b*) fatty acids from original tree in Table 2 and Fig. 1 (proportion of total variation explained by each discriminant axis = 0.91, 0.075, 0.015), and (*c*) fatty acids chosen from tree constructed on fatty acids used by Grahl-Nielsen and Mjaavatten (1991) (proportion of total variation explained by each discriminant axis = 0.88, 0.07, 0.05).

	Predicted			
Observed	Day 0	Days 4–7	Days 12–14	Days 19–21
(*a*) Misclassification rate = 6/51 (no. of fatty acids = 5)				
Day 0	15	0	0	0
Days 4–7	0	15	0	0
Days 12–14	0	1	9	2
Days 19–21	0	0	3	6
(*b*) Misclassification rate = 8/51 (no. of fatty acids = 7)				
Day 0	14	1	0	0
Days 4–7	2	13	0	0
Days 12–14	0	1	9	2
Days 19–21	0	0	2	7
(*c*) Misclassification rate = 12/51 (no. of fatty acids = 5)				
Day 0	13	2	0	0
Days 4–7	2	12	1	0
Days 12–14	0	2	9	1
Days 19–21	0	0	4	5

from applying the tree constructed from 1990 data to these 1993 data was 5/15 or 0.333, in the low end of the range predicted by the 10-fold cross-validation (Table 3). All of the Day 0 observations were correctly and consistently classified using 16:2*n*–6; however, the Days 19–21 samples were misclassed as either Days 4–7 or 12–14.

Linear discriminant analysis has also been used to classify tissue fatty acid samples (Grahl-Nielsen and Mjaavatten 1991). However, with fatty acid signatures, there are usually too many variables relative to the number of observations for discriminant analysis to be applied to the entire data set. Even stepwise variable selection for discriminant analysis requires the entire data set be used (Lachenbruch 1975). One approach has been to choose a subset of the most abundant fatty acids (Grahl-Nielsen and Mjaavatten 1991). We compared the results of stepwise linear discriminant analysis using Grahl-Nielsen and Mjaavatten's (1991) choice of the 18 most abundant fatty acids with those from the classification tree analysis. In addition, we investigated the use of the classification tree for choosing a subset of fatty acids for linear discriminant analysis by using either the seven fatty acids selected by the original tree (Table 2) or the five chosen by fitting a tree to the group of the 18 most abundant fatty acids.

The linear discriminant function based on Grahl-Nielsen and Mjaavatten's (1991) subset of fatty acids had the lowest misclassification error rate (resubstitution estimate = 6/51) of the three applications (Table 4*a*). The first of the five fatty acids chosen by the stepping algorithm (Wilks Λ) was 16:0, which was also chosen by the classification tree (Fig. 1) but was removed from the pruned tree (Fig. 4). Recall that deliberately

Table 5. Predictions from discriminant functions in Table 4 for the 1993 sample: (*a*) fatty acids chosen from subset given in Grahl-Nielsen and Mjaavatten (1991), (*b*) fatty acids from original tree in Table 2 and Fig. 1, and (*c*) fatty acids chosen from tree constructed on fatty acids from subset given in Grahl-Nielsen and Mjaavatten (1991).

	Predicted			
Observed	Day 0	Days 4–7	Days 12–14	Days 19–21
(*a*) Misclassification rate = 3/15				
Day 0	9	1	0	0
Days 19–21	1	0	1	3
(*b*) Misclassification rate = 2/15				
Day 0	10	0	0	0
Days 19–21	0	0	2	3
(*c*) Misclassification rate = 9/15				
Day 0	4	0	6	0
Days 19–21	0	1	2	2

choosing this fatty acid for the first node of a classification tree resulted in a tree with the same misclassification error as the trees in Figs. 1 and 4. None of the other fatty acids chosen by the stepwise linear discriminant analysis matched those chosen by the tree algorithm.

The discriminant function for the seven fatty acids chosen by the original tree had a slightly higher misclassification rate of 8/51 (Table 4*b*). However, the discriminant analysis based on the five fatty acids chosen by the classification tree from 18 major fatty acids (Table 4*c*) had a higher misclassification error rate (12/51) than the classification tree (9/51) based on these same five fatty acids.

Application of all three discriminant functions to the 1993 sample showed that the first two had similar misclassification error rates whereas the third function had a considerably higher rate (Table 5). The first two discriminant functions had lower misclassification rates for the 1993 sample than the pruned tree (Table 3). On the other hand, the classification tree used to choose the fatty acids for the third discriminant function actually had a better misclassification rate (4/15) for the 1993 data than did the discriminant function based on these same fatty acids (9/15).

Discussion

Our results indicate that classification trees of milk fatty acids can be a useful tool in evaluating differences or changes in foraging patterns of individuals within a population, as has also been demonstrated in another species of seal (Iverson et al. 1997). In fact, it appears quite feasible to use milk fatty acids to estimate lactation stages in harbour seal populations where it may be difficult to tag pups at birth. The change from initial fasting to feeding in lactating harbour seal females has direct implications for differences in the uptake and secretion of milk fatty acids by the mammary gland, and these appear to be readily distinguished using classification trees.

In the lactating harbour seal, milk secreted during the initial 6 days postpartum should be derived almost entirely from blubber and thus represent an integration of diet during the fattening period prior to parturition. Milk secreted subsequently during foraging trip intervals should include fatty acid influx from the immediate diet (Iverson and Oftedal 1992,

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1995; Iverson 1993; Iverson et al. 1995*a*, 1995*b*). If diet differs before and during lactation, then we would expect to detect changes in milk fatty acid composition. Indeed, in the females sampled in 1990, the tree analysis successfully classified most milk samples based on fatty acid composition into four lactation stages assigned by day of collection (Figs. 1 and 4). These results are consistent with our current understanding of the behaviour of female harbour seals during lactation, indicating that females begin foraging after about 6 days postpartum. We know that individual females may begin to feed as early as 2 days or as late as 14 days after parturition (Boness et al. 1994). Thus, we should expect to find variation among females, particularly during the Days 4–7 period, which may reflect interannual variation of the onset of foraging. Similarly, given that most females begin increasingly deeper and longer dive bouts after 11 days postpartum, indicating more intensive feeding, we would expect changes in fatty acids to be somewhat cumulative such that Days 12–14 and 19–21 milks would be more difficult to distinguish from one another, but to be readily distinguished from the fasting period. This was clearly the case in Fig. 4.

Based on lavage data obtained from Sable Island, harbour seal females are believed to feed predominantly on northern sand lance (*Ammodytes dubius*) throughout the 24-day lactation period (W. D. Bowen, unpublished data). Although little is known about the distribution of female harbour seals at other times of the year, tag recoveries suggest a rather wide distribution throughout the Scotian Shelf including the waters near Sable Island. Thus, there is reason to expect that the species composition of female diets may differ prior to and during the breeding season. Support for these differences is suggested by the observed changes in fatty acid composition of female milks. For instance, steady increases over lactation in components such as 20:1*n*–9, 22:1*n*–11, and 24:1*n*–9 may reflect the generally high levels of these fatty acids found in northern sand lance (unpublished observations).

Misclassification error rates calculated by the resubstitution method were more optimistic than the estimated rates produced by the 10-fold cross-validation and leave-one-out methods. However, the latter rates were closer to the observed rate of misclassification for the 1993 sample. Given the range of misclassification rates that can be obtained from the cross-validation method (Fig. 5), it may be more useful to calculate a number of realizations when evaluating the potential future performance of a tree.

A more relevant test of value of classification trees to the ecological analysis of milk fatty acid signatures was our ability to predict lactation stage (i.e., fasting versus feeding) of females in another year (3 years later). Despite potential interannual variation in diet, most milks from the 1993 season were correctly separated into fasting versus feeding based on the 1990 classification rules. The clear distinction of Day 0 milks from later foraging milks and the classification of Days 19–21 milks into "foraging milks" (mostly Days 12–14) is consistent with the foraging patterns of lactating females.

Several points are evident from our comparison of discriminant analysis with classification trees. First, when confined to the same group of fatty acids chosen by the original tree, the resubstitution misclassification rate for the discriminant function was not much better than that for the classification tree. However, this discriminant function did outperform the classification tree when predicting the categories for the 1993 tree. If this advantage was to hold in general, then classification trees may offer a means for choosing fatty acids for the linear discriminant analysis. However, our results from using the classification tree to choose fatty acids from the 18 given by Grahl-Nielsen and Mjaavatten (1991) suggest that discriminant analysis will not always outperform classification trees. Lynn and Brook (1991) compared the cross-validation misclassification error rates from classification trees and discriminant analysis for 12 data sets. They tentatively concluded that classification trees performed as well or better for the cases where there were large data sets with complex structure or heterogeneous covariance structures. In such cases, the assumptions of linear discriminant analysis may often be violated. Discriminant analysis outperformed classification trees for the smaller data sets studied by Lynn and Brook (1991).

The discriminant analysis based on the fatty acids used in Grahl-Nielsen and Mjaavatten (1991) provided a resubstitution misclassification error rate similar to that of the pruned tree. Only one of the 18 major fatty acids, 16:0, given by Grahl-Nielsen and Mjaavatten (1991) was chosen by the algorithm for the original tree. In fact, it was one of the less abundant fatty acids, 16:2*n*–6, that by itself was so effective in classifying the Day 0 samples for both the 1990 and the 1993 data sets. This serves to underscore the potential loss of information that could result from analysing only the most abundant fatty acids.

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Toxicological mechanisms of a multicomponent agricultural seed protectant in the rainbow trout (*Oncorhynchus mykiss*) and fathead minnow (*Pimephales promelas*)

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Abstract: Ethylene glycol (EG) and thiram, an aldehyde dehydrogenase inhibitor, are components of the seed protectant Vitavax-200. EG is a common solvent, thought to be nontoxic, whereas thiram, a dithiocarbamate known to be toxic to fish, is an active ingredient in Vitavax-200. When the toxicities of EG and thiram were investigated individually and as a mixture in rainbow trout (*Oncorhynchus mykiss*) and fathead minnow (*Pimephales promelas*), a strong synergistic toxic effect was observed. Using a constant sublethal concentration of thiram, a 5- to 19-fold increase and a 2- to 2.4-fold increase in EG toxicity was observed in fathead minnow and rainbow trout, respectively. The toxicity of EG following pretreatment of rainbow trout with pyrazole, an alcohol dehydrogenase inhibitor, was decreased by 22% whereas pretreatment with cyanamide, an aldehyde dehydrogenase inhibitor, increased toxicity 3.4-fold. The results indicate that thiram inhibits the complete metabolism of EG, resulting in the buildup of a toxic aldehyde intermediate and increasing the toxicity of EG.

Résumé : L'éthylèneglycol (EG) et le thirame, un inhibiteur de l'aldéhyde déshydrogénase, sont des produits qui entrent dans la composition du sécuriseur de semences Vitavax-200. L'EG est un solvant courant, que l'on croit non toxique, alors que le thirame, un dithiocarbamate reconnu toxique pour les poissons, est un ingrédient actif de Vitavax-200. Lorsque la toxicité de l'EG et du thirame a été étudiée individuellement et en mélange chez la truite arc-en-ciel (*Oncorhynchus mykiss*) et la tête-de-boule (*Pimephales promelas*), un effet toxique synergique important a été observé. À une concentration sublétale constante de thirame, on a observé des augmentations de la toxicité de l'EG de l'ordre de 5–19 fois et de 2–2,4 fois respectivement chez la tête-de-boule et la truite arc-en-ciel. La toxicité de l'EG après pré-traitement de la truite arc-en-ciel au pyrazol, un inhibiteur de l'aldéhyde déshydrogénase, a diminué de 22%, alors que le pré-traitement au cyanamide l'a augmentée par un facteur de 3,4. Les résultats indiquent que le thirame inhibe le métabolisme complet de l'EG, ce qui entraîne l'accumulation d'une intermédiaire aldéhyde toxique et une augmentation de la toxicité de l'EG.
[Traduit par la Rédaction]

Introduction

An accidental spill of Vitavax-200 (Uniroyal Chemical) in the Little Salmon River, Idaho, resulted in a fish kill that severely damaged the natural resources of the river for 24 miles (1 mile = 1.6 km) below the spill site (Idaho Department of Fish and Game 1988). Vitavax-200 is an agricultural formulation used to prevent fungal growth on seeds and is known to be highly toxic to fish because it contains the dithiocarbamate thiram. The extensive toxic effects observed following the spill may have been the result of interactions between the various components of the formulation, referred to as synergism (Marking 1985). The synergistic interaction between two or more chemicals can result in toxicity that is greater than would be expected by the addition of the toxicities of the individual components.

No studies to date have examined the toxicological interaction among the components of Vitavax-200 in mammals or fish, although the toxicological mechanisms of the individual components, thiram (tetramethylthiuram disulfide), carboxin (5,6-dihydro-2-methyl-1,4-oxathin-3-carboxanilide), and ethylene glycol (EG) (1,2-ethanediol), are well known. A major source of thiram toxicity is the metabolic production of carbon disulfide which can react with amino, mercapto, and hydroxyl groups resulting in the inhibition of enzymes such as aldehyde dehydrogenase (ALDH), an important enzyme in the sequential oxidation of alcohols (Vasak and Kopeckey 1967; Sanny and Weiner 1987). EG is sequentially oxidized in the liver of mammals (Chou and Richardson 1978) producing the oxidation products glycoaldehyde, glycolate, and glyoxylate, the relative toxicity of the metabolites being glyoxylate > glycoaldehyde > glycolate > EG (Beasley and Buck 1980). Based on a direct correlation between mortality and urinary glycolate concentrations, Chou and Richardson (1978) concluded that glycolate (glycolic acid) is the major mediator of EG toxicity in rats. Glycoaldehyde was theorized to play an insignificant role in EG toxicity because of low concentrations in the plasma and urine.

Based on the mammalian data, we hypothesize that thiram interferes with the complete metabolism of EG in fish by inhibiting ALDH, which results in the buildup of toxic EG metabolites. To investigate the possible interaction between thiram and EG, we determined the toxicity (LC_{50}) of thiram

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Table 1. Comparative toxicity of thiram, ethylene glycol and thiram-EG mixture for two lots of fathead minnow (*Pimephales promelas*).

Lot	Chemical	LC_{50}[a]	95% CI[a]	Slope[b]
1	Thiram	54.9	49.1–61.1	60.3 A
1	EG	1.10	0.96–1.18	0.43 B
1	Thiram–EG mixture[c]	0.22[d]	0.13–0.36[d]	0.06 C
2	Thiram	148	117–156	117 D
2	EG	1.12	1.06–1.17	0.64 B
2	Thiram–EG mixture[e]	0.06[d]	0.00–0.11[d]	0.02 C

[a]LC_{50} and 95% CI units are M, except thiram (nM).

[b]Values followed by the uppercase same letter are not significantly different ($\alpha = 0.05$).

[c]Concentration of thiram in the mixture was 36.6 nM.

[d]LC_{50} and 95% CI reported are for EG in the presence of thiram.

[e]Concentration of thiram in the mixture was 95.6 nM.

and EG individually and then as mixtures. To investigate the mechanism of thiram–EG joint toxicity, we determined the toxicity (LC_{50}) of EG after altering the metabolism of EG by (1) inhibiting alcohol dehydrogenase (ADH) with pyrazole (1,2-diazole), thus blocking the production of EG metabolites, and (2) inhibiting ALDH with cyanamide which results in the buildup of EG metabolites.

Materials and methods

Reagent-grade thiram (99% purity) was obtained from Uniroyal. EG (99% purity) was obtained from Fisher Scientific (Fair Lawn, N.J.). Pyrazole, cyanamide, and dimethylsulfoxide (DMSO) (tissue culture grade, 99+% purity) were obtained from Sigma (St. Louis, Mo.). DMSO was utilized to make stock solutions of thiram and cyanamide for in vivo toxicity tests.

Two separate lots of fathead minnow (*Pimephales promelas*) fry (10–20 days old) were obtained from Florida Bioassay (Gainesville, FL 32609). The fish were 90–100 days old and weighed 0.098 ± 0.014 g (lot 1) and 0.127 ± 0.013 g (lot 2), respectively, when exposed. Both lots were maintained at 20–25°C in flowing dechlorinated city water.

Rainbow trout (*Oncorhynchus mykiss*) were obtained from the University of Washington Seward Park Hatchery (Seattle, Wash.) as eyed embryos. Embryos were hatched in a stainless steel basket suspended in a 100-L flow-through aquarium. Fry were fed on commercial baby trout chow following yolk-sac resorption. Juveniles were maintained in 700-L flow-through tanks in dechlorinated city water at 10–15°C. Experiments were conducted with two size/age classes of fish (small: 60–90 days old, 0.707 ± 0.155 g; large: 90–120 days old, 1.503 ± 0.495 g).

All 96-h static renewal toxicity tests were conducted in glass aquaria constructed with nontoxic aquarium-grade silicone. Mean water temperatures for fathead minnow and rainbow trout toxicity tests were 21 ± 1.0 and 12 ± 1.0°C, respectively. Dissolved oxygen was maintained at or above 8.0 $mg \cdot L^{-1}$ with an air stone. Mean pH for all tests was 7.00 ± 1.0 and photoperiod was 16 h light : 8 h dark.

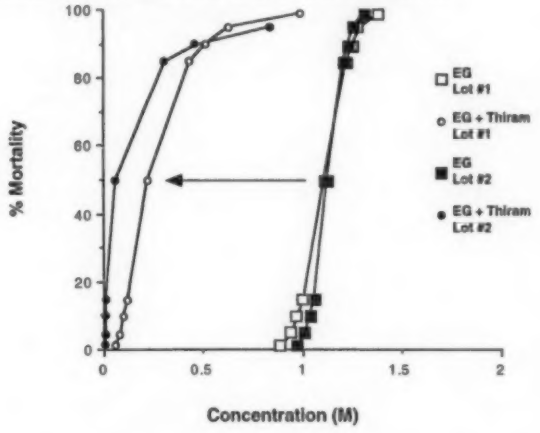
Test solutions were renewed daily with fresh stock solutions. Ten fish per tank (0.6–0.8 g $fish \cdot L^{-1}$) were used for all exposures and were allowed to acclimate unfed in the test aquaria for 24 h. For exposures involving thiram, solvent (DMSO) concentration did not exceed 0.1%. Four or five concentrations plus a control were utilized for each test, and mortalities were recorded and removed every morning and evening. Cumulative mortality was recorded over the 96-h period and the LC_{50} was calculated with the Probit Analysis Program, version 1.4 (EPA 1985). Student's *t*-test was used to test for differences between each pair of slope values from the linear probit regressions (Zar 1984).

To investigate the joint toxicity of thriam and EG, fish were exposed to a constant sublethal concentration of thiram added at the same time to four or five concentrations of EG plus a control, with dead fish recorded and removed every 12 h. Sublethal thiram concentrations, 36.6 and 95.6 nM for lot 1 and lot 2 of fathead minnow, respectively, and 0.15 and 0.17 µM for small and large rainbow trout, respectively, were first determined from the toxicity curves.

To evaluate EG toxicity after inhibition of ADH, rainbow trout were pretreated for 6 h with 0.10 M pyrazole (700 $mg \cdot L^{-1}$). Fish were exposed to four concentrations of EG plus a control in a static system for 96 h, with dead fish recorded and removed every 12 h. The LC_{50} was calculated after 96 h.

To evaluate EG toxicity after inhibition of ALDH in rainbow trout, the LC_{50} and toxicity curve were first determined for cyanamide. Fish were then pretreated for 6 h with a sublethal concentration of cyanamide, 1.19 mM (50 $mg \cdot L^{-1}$). Fish were exposed in a static system to four concentrations of EG plus a control for 96 h, with dead fish recorded and removed every 12 h. The LC_{50} was calculated after 96 h.

Fig. 1. Acute toxicity curves of EG and thiram–EG mixtures in juvenile fathead minnow. Calculations were based on the Probit Analysis Program, version 1.4 (EPA 1985). Mixture toxicity was determined by titrating EG while maintaining a constant sublethal concentration of thiram (36.6 nM, lot 1; 95.6 nM, lot 2).



Results

EG was more toxic ($P < 0.05$) in the presence of sublethal concentrations of thiram than when presented alone to fathead minnow (Table 1). No mortality was observed in untreated or DMSO-treated controls. In the presence of a constant sublethal concentration of thiram, the LC_{50} of EG decreased in lot 1 to 0.22 M and in lot 2 to 0.16 M, representing a 5- and 19-fold increase in toxicity, respectively (Fig. 1). In both lots of fathead minnow, the toxic response of the mixture extended over a wider range of concentrations than seen with individual toxicants.

The acute toxicity of EG also increased in rainbow trout in the presence of thiram. Toxicity was determined individually and as a mixture for two different sizes of rainbow trout (Table 2). Using a constant sublethal concentration of thiram, the LC_{50} of EG decreased in the smaller fish to 0.50 M whereas in the larger fish the LC_{50} decreased to 0.38 M (Fig. 2). The acute toxicity of thiram was the same in both sizes of rainbow trout; however, EG was more acutely toxic to the larger fish. No mortality was observed in untreated or DMSO-treated controls. The decrease in the LC_{50} represents a 2- and 2.4-fold increase in toxicity, respectively.

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Table 2. Toxicity of thiram, EG, and thiram–EG mixture for two size classes of rainbow trout and the effect of pyrazol and cyanamide on EG toxicity.

Size	Chemical	LC_{50}[a]	95% CI[a]	Slope[b]
Small	Thiram	0.26	0.24–0.28	0.09 A
Small	EG	0.98	0.95–1.00	1.37 B
Small	Thiram–EG mixture[c]	0.50[d]	0.46–0.54[d]	0.50 C
Small	EG–pyrazole[e]	1.11[d]	1.08–1.15[d]	1.10 B
Large	Thiram	0.27	0.24–0.30	0.06 A
Large	EG	0.91	0.86–0.94	0.61 B
Large	Thiram–EG mixture[f]	0.38[d]	0.34–0.41[d]	0.30 C
Large	Cyanamide	1.93	1.75–2.11	0.54 D
Large	EG–cyanamide[g]	0.27[d]	0.11–0.35[d]	0.07 C

[a] LC_{50} and 95% CI units are M, except thiram (μM) and cyanamide (mM).
[b] Values followed by the uppercase same letter are not significantly different ($\alpha = 0.05$).
[c] Concentration of thiram in the mixture was 0.15 μM.
[d] LC_{50} and 95% CI reported are for EG in the presence of thiram, pyrazole, or cyanamide.
[e] Concentration of pyrazole was 0.10 M.
[f] Concentration of thiram in the mixture was 0.17 μM.
[g] Concentration of cyanamide was 1.19 mM.

In both fathead minnow and rainbow trout, hyperpigmentation was associated with thiram toxicity and a narcotic effect was associated with EG toxicity. A narcotic effect similar to EG toxicity alone was associated with thiram–EG toxicity. Slopes of the linear probit regressions from EG-treated fish were different (*t*-test, $P < 0.05$) from those of fish treated with the thiram–EG mixture (Tables 1 and 2), indicating that toxicities from EG and thiram–EG are the result of different mechanisms.

In rainbow trout pretreated with pyrazole, the LC_{50} of EG increased by 22% (0.98–1.11 M) after 96 h (Fig. 3A). A 3.4-fold increase in EG toxicity occurred in rainbow trout pretreated with a sublethal concentration of cyanamide, an ALDH inhibitor, and subsequently exposed to EG. This was evident by a decrease in LC_{50} for EG from 0.85 to 0.27 M after 96 h (Fig. 3B). A broad response to EG after cyanamide pretreatment, evident from the slope, was similar to that observed in the thiram–EG mixture in fathead minnow, suggesting that EG was responsible for the observed toxicity (Table 2).

Discussion

Complex mixtures are often more toxic than can be predicted by summing the toxicity of their individual components. This study does not reject this hypothesis for Vitavax-200, where the toxicity of the carrier, EG, increases in the presence of an active ingredient, thiram. The toxicity of EG in fathead minnow increases 5- and 19-fold when a sublethal concentration of thiram is present whereas in rainbow trout the increase is 2- and 2.4-fold. Pretreatment with pyrazole, an ADH inhibitor, decreased the toxicity of EG by 22% in rainbow trout, presumably by blocking the conversion of EG to an aldehyde. Conversely, pretreatment of rainbow trout with cyanamide, an ALDH inhibitor, increased the toxicity of EG 3.4-fold by presumably blocking the detoxification of aldehyde intermediates. It is proposed that in rainbow trout and fathead minnow, ADH bioactivates EG to a more toxic intermediate, and the

Fig. 2. Acute toxicity curves of EG and thiram–EG mixtures in juvenile rainbow trout. Calculations were based on the Probit Analysis Program, version 1.4 (EPA 1985). Mixture toxicity was determined by titrating EG while maintaining a constant sublethal concentration of thiram (0.15 μM, small fish; 0.17 μM, large fish).

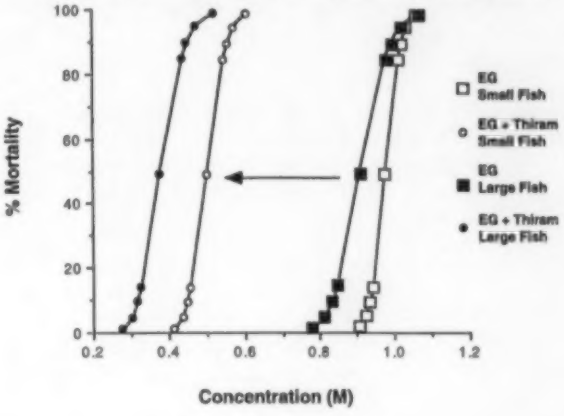
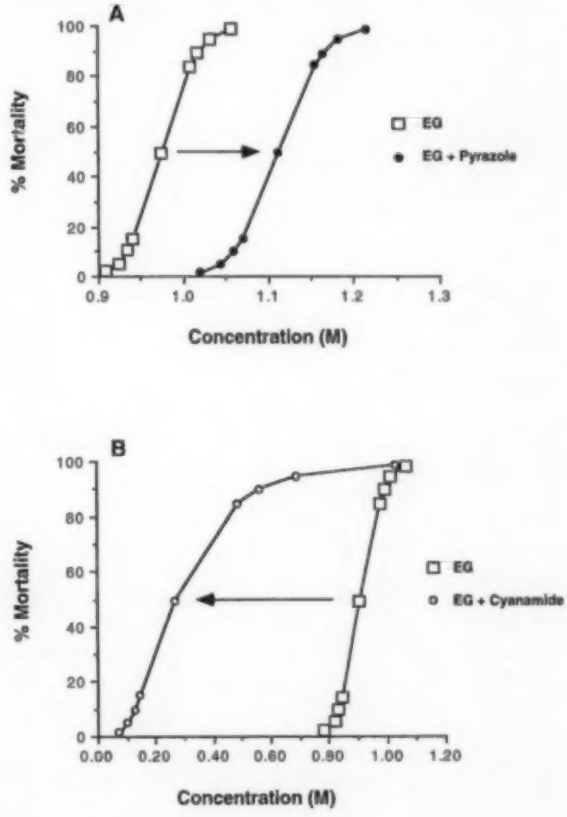


Fig. 3. Acute toxicity curves for (A) EG and EG–pyrazole pretreatment and (B) EG and EG–cyanamide pretreatment in juvenile rainbow trout. Toxicity curves were calculated with the Probit Analysis Program, version 1.4 (EPA 1985).



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mechanism of EG-enhanced toxicity by thiram is the inhibition of aldehyde metabolism.

Thiram was about six times more toxic in fathead minnow than in rainbow trout of a similar age but different size. Previously, EG was found to be less toxic to small rainbow trout (0.70 g) with an LC_{50} of 0.74 M compared with an LC_{50} of 0.29 M in larger rainbow trout (1.10 g) (U.S. Fish and Wildlife Service 1986), even though the response is thought to be directly related to size (Anderson and Weber 1975). Our results are in agreement with the observation that response to EG is inversely related to size in rainbow trout. In the present study, genetic stock and test conditions were constant whereas size was variable, yet EG was more acutely toxic to larger fish. It is unlikely that DMSO had any toxic effect because it has been used as a carrier for thiram in in vitro enzyme assays in rainbow trout and concentrations of 0.1% did not significantly affect three different liver antioxidant enzyme activities (Babo and Vasseur 1992).

Metabolic inhibitors are used to identify metabolic pathways by blocking specific reactions in vivo so that the pathway of the reaction can be identified. We have taken advantage of two inhibitors that have been found to block the initial oxidation of EG to glycoaldehyde, catalyzed by ADH, and the subsequent oxidation of glycoaldehyde to glycolate, catalyzed by ALDH. Pyrazole has been used as an ADH inhibitor, decreasing the toxicity of EG in rats by reducing the serum level of the metabolite glycolate (Chou and Richardson 1978). Pyrazole has also been used to prevent formation of a hepatotoxic intermediate in allyl formate metabolism by inhibiting ADH in adult rainbow trout (Droy et al. 1989). In this study, inhibition of ADH by pyrazole decreased the toxicity of EG in rainbow trout, presumably by reducing the formation of toxic intermediates. Cyanamide has been used as an inhibitor of ALDH in mammalian systems (Marchner and Tottmar 1978; DeMaster and Stevens 1988). In the present study, inhibition of ALDH in rainbow trout was associated with an increase in the toxicity of EG, similar to the toxicity observed in the thiram–EG mixture. The slope values from the linear probit regressions were not significantly different, suggesting that a similar mechanism is shared that is different from the mechanism of EG alone. In rats, Marchner and Tottmar (1978) observed a two- to threefold increase in acetaldehyde, the first oxidation product of ethanol metabolism in vivo, after administering ethanol and cyanamide. In rainbow trout, inhibition of ALDH by cyanamide or thiram prior to EG exposure should also result in increased glycoaldehyde formation. Aldehydes such as glycoaldehyde have been found to cross-link to amino acids and proteins such as collagen, serum albumin, and lipase and have a wide range of physiological effects such as altering the metabolism of serotonin, release of histamine, and inhibition of the oxidative process in the mitochondria (Schauenstein et al. 1977; Acharya and Manning 1983).

The mechanism of EG toxicity in fish is suspected to result from the production of toxic metabolic intermediates. This mechanism appears to be different from the mechanism of thiram–EG joint toxicity based on significant differences in the slope values from the thiram–EG joint toxicity and EG toxicity linear probit regressions and the up to 19-fold increase in thiram–EG joint toxicity. Based on the known effects of dithiocarbamates on alcohol metabolism, thiram–EG joint toxicity is proposed to result from the accumulation of glycoaldehyde.

Even though inert ingredients are currently regulated in pesticide formulations, a more detailed analysis should be undertaken to investigate interactions of these chemicals with the active ingredients within pesticide formulations. A better understanding of the mechanisms of mixture toxicity to aquatic organisms may lead to alternative formulations that are less toxic.

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Differentiation of rainbow trout (*Oncorhynchus mykiss*) populations in Lake Ontario and the evaluation of the stepwise mutation and infinite allele mutation models using microsatellite variability

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Abstract: Microsatellites, comprising $(GT)_n$ tandemly repeated arrays, were isolated from a size-selected genomic library of rainbow trout (*Oncorhynchus mykiss*) DNA. Primers were designed for five microsatellite loci, four of which were variable. Primers for two of these loci were used in conjunction with primers for three microsatellite loci from a related species, *Salmo salar*, to investigate patterns of differentiation in freshwater migratory populations of rainbow trout in Lake Ontario. The five loci used revealed high levels of polymorphism with heterozygosity estimates ranging from 0.740 to 0.956. Significant differences in allele frequencies among populations were observed for all loci. Heterozygosity and allele number values, at each locus for each population, were used to test two alternative mutation models, the infinite allele model (IAM) and the stepwise mutation model (SMM). The predictions of the IAM proved to be more accurate for the majority of the data and this model was used to calculate estimates of effective population size.

Résumé : Des microsatellites, comprenant des séquences $(GT)n$ répétées en tandem, ont été isolés d'une banque génomique d'ADN de truite arc-en-ciel (*Oncorhynchus mykiss*) sélectionnés en fonction de la taille. Des amorces ont été conçues pour cinq loci de microsatellites, dont quatre variables. Les amorces pour deux de ces loci ont été utilisées avec des amorces pour trois loci de microsatellites d'une espèce apparentée, *Salmo salar*, pour étudier les motifs de différenciation dans les populations migratrices d'eau douce de truites arc-en-ciel dans le lac Ontario. Les cinq loci utilisés ont révélé de hauts degrés de polymorphisme avec des estimations de l'hétérozygotie variant entre 0,740 et 0,956. Des différences significatives dans les fréquences d'allèles entre les populations ont été observées pour tous les loci. Les valeurs de l'hétérozygotie et du nombre d'allèles, pour chaque locus dans chacune des populations, ont été utilisées pour tester deux modèles possibles de mutation, le modèle d'allèles infinis (MAI) et le modèle de mutation par étape (MME). Les prévisions faites par le MAI se sont révélées plus précises pour la plupart des données et ce modèle a été utilisé pour calculer les valeurs estimées de la taille réelle de la population.
[Traduit par la Rédaction]

Introduction

The application of genetic markers has revolutionized the management of many species. Allozymes have been the traditional tool used to define population structure in fishes (e.g., Shaklee et al. 1990; Miller et al. 1993). However, despite the success of allozymes in population genetics (Utter 1991), this type of marker has failed to detect significant levels of polymorphism in many species that have undergone population bottleneck events and (or) captive breeding programs (Bonnell and Selander 1974; O'Brien et al. 1983).

For this reason, workers began to utilize more variable DNA-based marker systems. Initially, the analysis of mtDNA was used to investigate questions of population structuring in a wide range of organisms (see Avise 1989 and references therein). Interest in this molecule was generated by the observation of an evolutionary rate 5–10 times that of single-copy nuclear DNA in vertebrates (Brown et al. 1979) and initial observations of distinct geographic clustering of haplotypes (Avise et al. 1979). However, in species with a high capacity for dispersal, much lower levels of divergence are usually observed (see Avise et al. 1987; Ball et al. 1988). Moreover, the tight linkage of genes in the mitochondrial genome means that all mtDNA variation is analogous to variation at a single locus (Wilson et al. 1987).

As random drift will affect different loci in a stochastic fashion, estimates of genetic relatedness between populations should be based on several loci (Nei 1987; Palumbi and Baker

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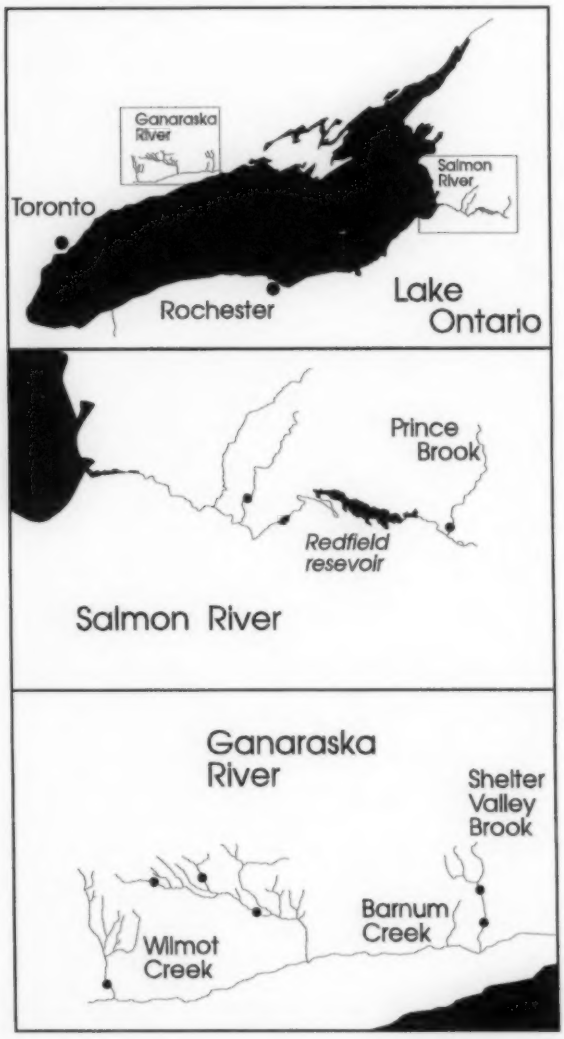
Fig. 1. Sampling sites (circles) around Lake Ontario. The insets show the distribution of sample sites within Ontario and New York in more detail.



1994). Due to their abundance and highly polymorphic nature, microsatellites are being increasingly used to address population genetic questions (e.g., Roy et al. 1994). Microsatellite DNA is composed of short (2–5 base pairs (bp)), tandemly repeated arrays that appear to be widely dispersed in the eukaryote genome (Tautz and Renz 1984; Tautz 1989). These loci can be investigated using the polymerase chain reaction (PCR) which is technically simple and permits the use of small and (or) degraded samples of tissue or DNA. These properties, in conjunction with the very high levels of heterozygosity found at these loci (Tautz 1989; Brooker et al. 1994), make microsatellite DNA an ideal marker system for many population genetic questions.

Two models of mutation generally proposed to account for variation at microsatellite loci are the stepwise mutation model (SMM) and the infinite allele mutation model (IAM). The models differ in that the SMM predicts that mutation occurs through the gain or loss of a single repeat unit, e.g., GT. This means that some mutations will generate alleles already present in the population. In contrast, the IAM predicts that mutation can only lead to new allelic states and may involve any number of repeat units. The value to fishery managers of determining which model provides a better overall fit to the data is that it facilitates more accurate estimates of population size (Estoup et al. 1995).

Rainbow trout (*Oncorhynchus mykiss*) are naturally distributed along the west coast of North America from Alaska to Mexico and water bodies west of the continental divide (Behnke 1979). Rainbow trout display a broad array of life history strategies, e.g., anadromy versus residency, variation in age and time of maturation, precocious development, diet, etc. (Behnke 1979). The species' ability to tolerate transfer into unoccupied but suitable habitats is primarily responsible for its present worldwide distribution (Gall and Crandell 1992). Since the 1870s, rainbow trout, predominately derived from the McCloud River in northern California, have been transplanted and reared worldwide (Dollar and Katz 1964). The first transfer of rainbow trout outside their natural distribution range occurred in 1874 when eyed eggs from the McCloud River were shipped to the Caledonia hatchery in New York (Hershberger 1992). Coastal anadromous rainbow trout (steelhead) represented the majority of these transfers (Needham and Behnke 1962). In the late 1870s, rainbow trout from this hatchery were introduced into Lake Ontario for the first time (MacCrimmon 1971). Since that time, rainbow trout from many sources have been planted into the Great Lakes. The species has now established self-sustaining populations throughout the Great Lakes region. Many of these populations are potadromous, with individuals feeding in the Great Lakes before returning to a riverine environment to spawn.

The primary objective of this paper is to report on the levels of genetic variability and divergence at five microsatellite loci from five populations of rainbow trout within Lake Ontario. We also compare the predictions of the SMM and IAM with the observed data. Finally, the microsatellite data are also compared with the results of a previous mtDNA survey of these populations.

Materials and methods

Sample collection

Samples were collected from three rivers within Ontario and two within New York State (Fig. 1). Juvenile fish (10–20 cm) were collected by various methods. Juveniles from the Salmon River and Prince Brook sites were collected in August 1993 by electrofishing. Fish from Wilmot Creek were also collected by electrofishing in May 1992, while the remainder of the samples were collected by angling in the summers of 1993 and 1993. Juveniles from the Ganaraska River were collected from three sites on the upper section of the river in order to increase the sample size. Samples were transported on ice to the University of Guelph. Muscle tissue was stored at –80°C before the DNA was extracted by standard phenol–chloroform techniques (Sambrook et al. 1989).

Library construction and screening

Fifty micrograms of genomic DNA from two rainbow trout individuals was digested with *Sau*3AI. The 500–800 bp size fraction was

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recovered from a 1% agarose gel using standard techniques and ligated into dephosphorylated pUC18 (Pharmacia) cut with *Bam*HI. A second library was also constructed from an *Alu*I, *Hin*cII, *Hae*III, *Rsa*I digest. This was ligated into dephosphorylated pUC18 (Pharmacia) cut with *Sma*I. "Max-efficiency" DH5α cells (GIBCO BRL) were transformed according to the supplier's instructions, inoculated on selective media (AMP^+), and colonies fixed to nylon membranes (Hybond N) according to the manufacturer's recommendations (Amersham). The membranes were prehybridized for 2 h in 5× SSPE, 0.1% SDS, 5× Denhardt's, and 10 μg RNA/mL at 65°C. A $(GT)_{15}$ oligonucleotide was labelled with T4 polynucleotide kinase (PNK) (Pharmacia) and [γ-^{32}P]ATP for 30 min at 37°C. The oligonucleotide probe was added to the hybridization mixture and the hybridization carried out at 65°C overnight. Membranes were washed twice at room temperature and once at 55°C in 2× SSPE and exposed to X-ray film, with intensifying screens, for 6 h at –80°C. Hybridizing colonies were picked and grown up for 36 h. A sample of the culture was used to prepare glycerol stocks and stored at –80°C, while the remainder was used as template for sequencing. The plasmid DNA was extracted using an alkaline-lysis procedure (Sambrook et al. 1989). Sequencing was carried out using a T7 sequencing kit (Pharmacia) in the forward and reverse directions.

PCR conditions

Two of the loci, *Omy325* and *Omy207*, were analyzed by direct incorporation of α-^{35}S during PCR according to the methods of Estoup et al. (1993). The concentration of each dNTP was 100 and 0.5 μM of each primer. For all other loci, the B (reverse) primer was labelled using PNK and [γ-^{32}P]dATP for 30 min at 37°C. PCR reactions were carried out in 10-μL volumes in a 96-well microtitre plate (COSTAR). Working concentrations were as follows: 0.6 μM forward primer, 0.56 μM reverse primer, 0.04 μM labelled reverse primer, 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 0.001% gelatin, 1.0 mM $MgCl_2$, 200 μM each of dATP, dCTP, dGTP, and dTTP, 0.25 U of *Taq* polymerase, and 10–20 ng of template DNA. The amplifications were carried out in an MJ thermal cycler (MJ Research Inc.). For the first five cycles, denaturation was carried out at 94°C for 20 s, the annealing step was carried out at the specific primer optimum for 20 s, and extension was carried out at 72°C for 20 s. In subsequent cycles (35–40) the denaturation temperature was reduced to 90°C. When the amplification was complete, an equal volume of deionized formamide stop dye (Pharmacia) was added to each reaction well. The products were denatured at 95°C for 15 min and separated on an 8% 30 × 40 cm sequencing gel. After fixing and drying the gel for 1 h, the gel was exposed to X-OMAT-AR film (Kodak) overnight without screens. The sizes of PCR products were estimated by reference to amplified control samples and a M13mp18 sequencing reaction that was run on each gel as a standard.

Statistical analysis

Heterozygosity was estimated using Nei's (1987) unbiased estimate. A global χ^2 test was used to examine allele frequency heterogeneity among sites using the Markov Chain (MC) method (Guo and Thompson 1992) with the computer program GENEPOP version 1.2 (Raymond and Rousset 1994). GENEPOP was also used to test whether the genotype proportions in each population conformed to Hardy–Weinberg (HW) expectations using the exact HW test of Guo and Thompson (1992) (see Raymond and Rousset 1994 for details). FSTAT version 1.2 (Goudet 1996) was used to calculate the f_i and θ coefficients (Weir and Cockerham 1984). The standard deviation and confidence limits (95 and 99%) associated with θ were generated through jack-knifing and bootstrapping (1000 replicates), respectively (see Dallas et al. 1995). The number of migrants (N_{em}) was estimated using the private allele model (Barton and Slatkin 1986) and from the θ coefficient (Wright 1978). Both of these estimates are based on an island model of migration and assume that all loci and populations are in mutation drift equilibrium. Not all these assumptions are realistic and the results have to be considered with caution, although the estimates do serve as a useful relative measure to compare among populations. The relationships between all pairs of populations were investigated using a Cavalli-Sforza and Edwards (1967) chord distance. These values were then used to construct a neighbor-joining (NJ) tree (Saitou and Nei 1987). The genetic relationships between sites were also investigated by a maximum likelihood tree, built using the CONTML option in PHYLIP (Felsenstein 1993). Bootstrap values for trees were calculated from 1000 replications resampling across loci.

To test the predictions of both mutation models the expected number of alleles and expected heterozygosity for both models were calculated. The expected number of alleles under the IAM was calculated according to Ewens' (1972) such that $k_e = 1 + M/(M+1) + M/(M+2) + ... + M/(M+n-1)$, where $M = 4N_e\mu$, N_e and μ being the effective population size and locus mutation rate, respectively. At equilibrium, $M \approx H(1-H)$, where H denotes heterozygosity (Crow and Kimura 1970). As H may be biased when based on a single locus (Zouros 1979), a bias-corrected estimator of M was found by solving the equation $M^3 + (7 - M_o)M^2 + (8 - 5M_o)M - 6M_o = 0$ in which $M_o = H_o/(1 - H_o)$ (Chakraborty and Weiss 1991).

The expected heterozygosity under the IAM was calculated by solving Ewens' equation above for an observed value of k that leads to a corresponding M value (H_e deduced as $[M/(1+M)]$.

The expected number of alleles under the SMM was estimated by first calculating a bias-corrected estimator of M (Zouros 1979) such that $1.7M^4 + (25 - 1.7M_o)M^3 + (24.5 - 13M_o)M^2 + (9 - 22.5M_o)M - 6M_o = 0$, where $M_o = 0.5[(1 - H_o)^{-2} - 1]$ (Ohta and Kimura 1973). Using numerical integration, the equilibrium distribution of allele frequencies ($\Phi(x)$) was calculated (for details, see Kimura and Ohta 1978; Estoup et al. 1995). Ewens' (1972) rationale was then used to estimate the average number of alleles in a sample of n genes by integrating $[1 - (1 - x)^n]\Phi(x)dx$ on the same interval $1/(2N),1$, where the value of N was optionally set at 1000 in all cases. This latter integral was found through numerical integration (in steps of 10^{-5}). The expected heterozygosity under the SMM was obtained by calculating H_e for two extreme values. The next step was to find the corresponding number of alleles through the method outlined above and to reduce the difference between the observed number of alleles and the calculated value through an iterative process until the gap between both values of H_e was less than 10^{-3}. The probability that the observed number of alleles and heterozygosity values are as or more different from the values predicted by both models was calculated through computer simulations (1000 replicates) of the coalescent process of sampled genes (J.-M. Cornuet, unpublished data). The effective population sizes of the five populations and mutation rates at the five loci were estimated simultaneously according to Chakraborty and Neel (1989). This method assumes that the loci evolve under the IAM and that the populations are in mutation drift equilibrium. As only the product $N_e\mu$ can be estimated, the calculations were carried out under the constraint that the geometric mean of the mutation rate (μ) for the five loci was 10^{-4}.

Results

Genomic library and microsatellite loci

Approximately 4000 colonies were screened when the singly and multiply digested libraries were combined. One hundred and sixty positives were identified when screened with the GT repeat probe. However, on sequencing, only 128 positive clones could be described as microsatellites as defined by Weber (1990). The other clones contained repetitive sequences such as minisatellites or simple sequence repeats that were too small to be formally described as microsatellites. The 128 microsatellite-containing clones were further subclassified

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Table 1. Primer sequences, type of array amplified, and PCR conditions associated with each locus.

Locus	Primers (5′–3′)	Repeat	Annealing temperature (°C)
Omy278	ACTCCAGCACACCTGTCTCC TGTCTCAGTGCTCTTTCCC	$(GT)_{32}$	51
Omy287	TCCTGGTCTGGGCAGG	$(GT)_{26}$	51
Omy293[a]	CACAGAGTGCGATCGTGG GGTACTAATGTTAAGCTCGAG	$(GT)_{28}$	47
Omy325[a]	TGTGAGACTGTCAGATTTTGC CGGAGTCCGTATCCTTCCC	$(GT)_{22}$	50
Omy207[a]	ACCCTAGTCATTCAGTCAGG GATCACTGTGATAGACATCG	$(GT)_{31}$	53
Ssa85[a,b]	AGGTGGGTCCTCCAAGCTAC ACCCGCTCCTCACTTAATC	$(GT)_{20}$	57
Ssa293[a]	TGGTTATTTGTTTCCAGAG ATCAGATACACAGAGACGG	$(GT)_{49}$	55

[a]Loci used in the population survey.
[b]*Ssa85* first described in O'Reilly et al. (1996).

according to Weber (1990) as perfect ($n = 81$), imperfect ($n = 38$), compound perfect ($n = 5$), and compound imperfect ($n = 4$). The average colony insert size was 500 bp, and approximately 2.0×10^6 bp of the genome was investigated in the present screening effort. Therefore, one GT microsatellite was found on average every 15.6 kbp, assuming the arrays were randomly distributed throughout the genome.

Primers were designed for five microsatellite arrays (Table 1), which were chosen on the basis of size, type, and suitable flanking sequences. *Omy293* appeared fixed for one allele, and two of the remaining primers, *Omy278* and *Omy287*, appeared to amplify duplicate loci, and a genetic interpretation of inheritance patterns at these loci was unclear. The segregation of alleles at *Omy207* and *Omy325* was consistent with Mendelian segregation (unpublished research).

Heterozygosity and distribution of variation

Omy207 and *Omy325* were used in conjunction with three other microsatellite loci developed for Atlantic salmon (*Salmo salar*) (McConnell et al. 1995; O'Reilly et al. 1996) (Table 1). The average number of alleles per locus in all populations was high (Table 2). The heterozygosity values ranged from 0.740 for *Ssa85* at the Ganaraska site to 0.956 for *Ssa293* at Wilmot Creek (Table 2). The observed heterozygosity values at two sites, Ganaraska and Prince Brook, differed significantly from HW expectations. Both sites also showed the smallest number of alleles when averaged across the five loci. A global χ^2 test of allele frequency heterogeneity revealed significant differentiation at all loci among sites. The extent of differentiation, as estimated by θ, also appeared significantly different from zero (Table 3). The estimated number of migrants between all sites per generation, after correction for size of the microsatellite DNA data set (Barton and Slatkin 1986), was seven. The estimate derived from the θ value was more than twice this value (Table 3). When these estimates were calculated for both regions, the level of genetic exchange within New York was lower than for the Ontario estimates.

Genetic relationships

The unrooted NJ tree, constructed from the Cavalli-Sforza and Edwards (1967) chord distance, and the maximum likelihood tree have identical topologies (Fig. 2). Furthermore, the bootstrap values for both distance coefficients were almost identical in both trees. The largest bootstrap values for both trees (83/82) correspond to the branch point separating the sites from the two regions. Within the Ontario region, the Ganaraska site appeared to be the most genetically distinct.

Evaluation of mutation models

The expected heterozygosity and number of alleles for each population at each locus were calculated, based on the assumptions of the SMM and IAM (Table 4). In four of the populations (the exception is the Prince Brook site where mutation drift equilibria for all loci could not be rejected) the first three loci (*Omy325*, *Omy207*, and *Ssa293*) appeared to be in mutation drift equilibrium. This observation and the general fit of the data to HW expectations (which assumes mutation drift equilibrium) indicated that the data were appropriate for testing the mutation models. However, *Ssa85* exhibited a heterozygote deficiency for the Ganaraska and Salmon rivers and *Ssa4* revealed a similar deficit for the Salmon River, Wilmot Creek, and Shelter Valley sites after correcting for table-wide significance with a global threshold value of 0.05 (Rice 1989) (Table 4). Nevertheless, there did not appear to be any consistent excess or deficit of alleles across loci for any particular population. The predictions of allele number and heterozygosity based on the IAM uniformly proved to be more representative than the SMM. Therefore, we used Chakraborty and Neel's (1989) method, which is based on the IAM, to estimate the effective population sizes and mutation rates. The estimates of N_e were based on the assumption that the geometric mean of the mutation rate was 10^{-4} (Table 5). This estimate was used, as microsatellite mutation studies have estimated rates between 10^{-3} and 10^{-5} (Dallas 1992; Schlötterer and Pemberton 1994; Ellegren 1995). The geometric mean of N_e over loci was 20 012, with values ranging from 13 518 to 23 855 (Table 5). Despite the moderate size of the standard errors, it was still evident that the N_e estimate for Prince Brook was considerably smaller than for the other populations. The estimated mutation rates for the five loci ranged from 7.73×10^{-5} to 1.39×10^{-4}. Although the actual values are somewhat artificial (in that the geometric mean rate was constrained (10^{-4}) in the estimations), the comparative values are useful and revealed that the three *Ssa* loci had higher mutation rates than the two *Omy* loci (Table 5).

Discussion

Type and relative frequency of microsatellite arrays observed

In accordance with previously published reports, we have found $(GT)_n$ microsatellites to be extremely abundant in salmonids (Estoup et al. 1993; Sakamoto et al. 1994; McConnell et al. 1995). Approximately 62% of the microsatellites sequenced were perfect as defined by Weber (1990), and this agrees well with observations from other libraries constructed from rainbow trout and Atlantic salmon (Brooker et al. 1994; McConnell et al. 1995). The average size of the microsatellite

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Table 2. Allelic diversity, sample size, range of allele size, and the average heterozygosities at the five loci for the five populations investigated.

Population (sample size)		*Omy325*	*Omy207*	*Ssa293*	*Ssa85*	*Ssa4*
Prince Brook (20)	No. of alleles	11	16	9	13	20
	Het. (obs)	0.873	0.933	0.835	0.842	0.878
	Range (bp)	82–130	86–128	112–168	101–157	123–167
Salmon River (33)	No. of alleles	23	16	23	22	20
	Het. (obs)	0.928	0.909	0.928	0.853	0.811
	Range (bp)	80–136	84–128	96–172	97–169	113–189
Ganaraska River (30)	No. of alleles	14	15	20	16	20
	Het. (obs)	0.824	0.882	0.942	0.740	0.867
	Range (bp)	84–136	84–122	96–172	99–161	87–195
Wilmot Creek (30)	No. of alleles	17	16	27	16	16
	Het. (obs)	0.905	0.916	0.956	0.821	0.742
	Range (bp)	84–140	86–126	92–168	101–159	85–133
Shelter Valley (34)	No. of alleles	12	15	23	21	19
	Het. (obs)	0.805	0.809	0.955	0.888	0.769
	Range (bp)	84–130	84–128	96–172	101–171	107–1

Table 3. Mean estimates of the significance of θ after jack-knifing across five loci with standard deviations and 95% confidence limits generated through bootstrapping over 1000 replicates (estimates of N_{em} calculated using θ (Wright 1978) and the private allele method (Barton and Slatkin 1986)).

Regional grouping	θ	SD	95% confidence limits	99% confidence limits	N_{em} (Wright 1978)	N_{em} (Barton and Slatkin 1986)
Within New York	0.020	0.020	–0.004–0.057	–0.006–0.073	13	4
Within Ontario	0.012	0.003	0.007–0.017	0.006–0.019	25	5
New York vs. Ontario	0.009	0.003	0.004–0.013	0.003–0.014	27	6
Total estimate	0.016	0.004	0.009–0.024	0.009–0.026	18	7

loci sequenced was 28 repeat units. Although this is slightly lower than previous estimates for other salmonids (see Slettan et al. 1993), the high variance in the size of the arrays sequenced suggests that the difference is not significant.

Different models of mutation (IAM and SMM)

Table 4 reveals that *Ssa85* showed an excess of alleles under the IAM for the Salmon and Ganaraska rivers. *Ssa4* revealed a similar excess for the Salmon River, Wilmot Creek, and Shelter Valley sites. These excesses may be accounted for, if the loci on which the model's predictions are based do not agree with HW expectations. Although *Ssa4* is significantly different from HW expectations, this result is primarily due to the very low probability value associated with the Ganaraska site (f_i = 0.069, $P < 0.001$; Table 6). Therefore, we would not expect to observe the excess across sites other than the Ganaraska, which was the case. Another possibility that could explain the observed excesses is recent migration where the migrant and recipient gene pools had divergent allele frequencies at only *Ssa4* and (or) *Ssa85*. Thus, only these loci would show a deficit of heterozygotes, if an exchange of migrants occurred. However, this hypothesis is considered unlikely, as the two loci that showed a deficit of heterozygotes were those for which average distance values (averaged across all pairs of populations (data not shown)) were the smallest.

If we exclude *Ssa85* and *Ssa4*, Table 4 reveals that the IAM could not be rejected at any site. A comparison of the two models demonstrated that the estimated allele number and heterozygosity based on the IAM more closely resembled the observed data. This conclusion agrees with those of Estoup et al. (1995) who also observed that the IAM provided a better fit to their data. The estimates of N_e, based on the IAM, roughly averaged 20 000 (Table 4; estimates based on the SMM ($H = -(1/1 + 8N_e\mu)^{0.5}$; $m = 10^{-4}$; Ohta and Kimura 1973) would be considerably higher). Estimates of population numbers for the three Ontario rivers, based on electrofishing surveys, revealed similar numbers of juvenile fish for a given stream length. The population numbers for the three Ontario rivers are thought to range between 20 000 and 30 000, based on the assumption that the majority of fish passing the fishway on the Ganaraska River spawn (J. Bowlby, Ontario Ministry of Natural Resources, personal communication). Therefore, the N_e estimates derived from the IAM appear to approximate the census data. The overall fit of the data to the predictions of the IAM conflicts with earlier reports of microsatellite mutation processes (Edwards et al. 1992; Valdes et al. 1993; Weber and Wong 1993). Estoup et al. (1995) suggested that these differences might have been due to differences in the array type (perfect versus imperfect) used in various studies. Another possibility, given that only perfect type arrays were used in the present survey, may be the size of the repeat unit. Edwards et al. (1992) examined only trinucleotide and tetranucleotide loci. Shriver et al. (1993) observed this class of microsatellite loci to be more similar to the SMM relative to dinucleotide and minisatellite loci. Therefore, repeat unit size may also be an important component in deciding which of the mutation models may be more appropriately applied to a particular data set.

Intrapopulation variability

The rainbow trout populations investigated in the present study

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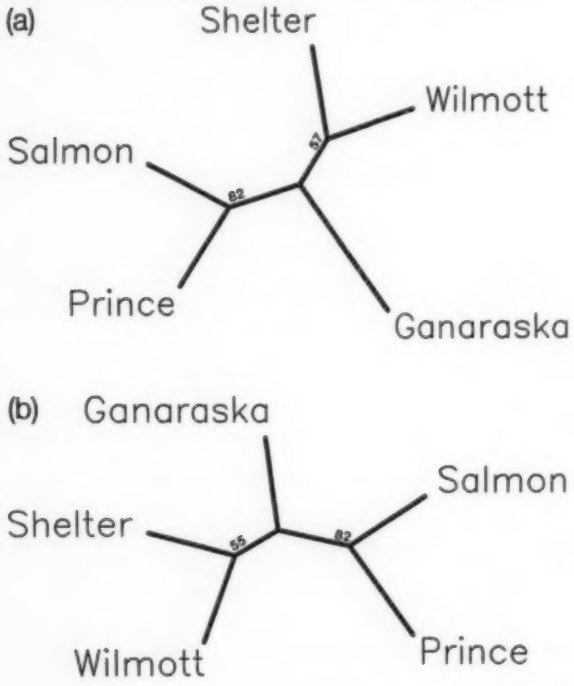
Fig. 2. Neighbor-joining and maximum likelihood trees constructed from (*a*) the Cavalli-Sforza and Edwards (1967) chord distance and (*b*) the CONTML option in PHYLIP (Felsenstein 1993). The numbers refer to bootstrap values generated over 1000 replications.



showed high levels of variability with an average heterozyosity value of 0.864. The number of alleles observed at each locus was higher than that observed by Nielsen et al. (1994) for *Omy77* in a population survey of rainbow trout within its native range. The high levels of variability may be due to the diverse origin of the populations investigated, as secondary introductions have occurred involving rainbow trout derived from areas other than the McCloud River, e.g., the Chambers Creek steelhead strain from Washington (Gall and Crandell 1992). Our results suggest that there have been no drastic losses of genetic variability associated with the introduction of rainbow trout to the area. This conclusion is further supported by the lack of a significant deficit of heterozygotes associated with any one site that would be indicative of a recent bottleneck (Maruyama and Fuerst 1984). These results are also consistent with observations of high levels of mtDNA diversity for these same populations (L.A. Dueck and R.G. Danzmann, unpublished data). However, we cannot definitely state that there has been no loss of genetic variation in the populations tested, as the loci investigated have not yet been applied to large, undisturbed reference populations in the wild. Moreover, workers should be cautious when comparing heterozygosities at highly variable loci, as even small differences can be significant.

The Ganaraska River and Prince Brook sites both had a significant deficit of heterozygotes when compared with HW expectations. The Ganaraska River population was collected from several sites throughout the catchment in order to increase the sample sizes. The significant deficit of heterozygotes observed for this sample site is probably due to a Wahlund effect (Wahlund 1928). This conclusion is consistent with the positive f_i values observed at all loci (four of which were significant) for this population (Table 6). The significant deficit of heterozygotes in the Prince Brook population may be due to a small effective population size. Although the estimate of N_e at this site may not be completely accurate (as it is based on the assumption that the geometric mean of the mutation rate is 10^{-4}), a comparison of the estimates for each site, i.e., the relative values, is informative. The estimate of N_e (based on the IAM) for the Prince Brook site was about half that of the other populations (Table 5). This result may be partly explained by a recent bottleneck. The likelihood of such an event is increased for this site relative to the others, as straying into this site is highly unlikely (site situated above several barriers to fish movement).

A molecular explanation, which has recently been proposed to account for deficits of heterozygotes at microsatellite loci, is the occurrence of null alleles (Pemberton et al. 1995). If a null allele occurs at a frequency p, the average number of individuals that would have to be sampled to observe one homozygote would be $E(N) = 1/p^2$. Thus, if $p = 10^{-2}$, $E(N) = 10\,000$ individuals, although the heterozygote deficiency generated by the null allele would be 0.02 ($2p$). Therefore, to account for a deficit of 0.1396 (average value for Ganaraska site), $p = 0.0698$, which means that one homozygote will be sampled for approximately every 200 individuals surveyed. Although this means that it is likely we would encounter a null allele, the significant deficit of heterozygotes at both sampling sites was seen for three loci. This suggests that null alleles are unlikely to be the sole agent responsible for the significant deviations.

When the levels of genetic variability were compared between the New York and Ontario populations, no significant difference in the level of heterozygosity was observed (t-test of mean arcsine transformed heterozygosity values). This contrasts with previous mtDNA surveys for the region that have revealed significantly less genetic variation within New York populations compared with those in Ontario (Danzmann et al. 1993; Dueck 1994). The observed differences between the nuclear and mtDNA markers may be due to the increased sensitivity of mtDNA to fluctuations in population size because of smaller effective population sizes.

Interpopulation divergence

Since their initial introduction approximately 120 years ago, rainbow trout have established self-sustaining spawning runs throughout the Great Lakes. The observed differences in allele frequencies between populations are probably due to stochastic events during colonization of new habitats, but although the number of generations is limited (40–50), we cannot exclude the possibility that populations have diverged at these rapidly evolving microsatellite loci through mutation. Individuals from these populations are probably returning to their natal sites to spawn, as significant allele frequency heterogeneity was observed at all loci using χ^2 probability values (excluding *Ssa4* ($P < 0.05$); all loci were associated with a highly significant probability value ($P < 0.0001$)) or when tested using θ values (Table 3). This observation is supported by the limited estimates of genetic exchange ($N_{em} = 7$ and 18 for private allele

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Table 4. Observed and expected number of alleles (k_o and k_e) and heterozygosity (H_o and H_e) under the infinite allele mutation model (IAM) and the stepwise mutation model (SMM).

Allele	n	k_o	H_o	k_e (IAM)	Pr (IAM)	k_e (SMM)	Pr (SMM)	H_e (IAM)	Pr (IAM)	H_e (SMM)	Pr (SMM)
Salmon River											
Omy325	60	19	0.891	16.2	0.222	10.9	0.002	0.907	0.208	0.934	0.008
Omy207	64	16	0.909	18.8	0.242	13.0	0.171	0.875	0.151	0.913	0.326
Ssa293	66	23	0.928	22.3	0.474	16.2	0.018	0.927	0.414	0.948	0.028
Ssa85	66	22	0.853	13.3	0.003	8.3	0.000	0.921	0.013	0.944	0.000
Ssa4	64	20	0.811	10.7	0.001	6.7	0.000	0.910	0.008	0.936	0.000
Prince Brook											
Omy325	36	11	0.873	11.8	0.455	8.8	0.207	0.845	0.321	0.881	0.277
Omy207	38	16	0.933	17.8	0.323	14.9	0.405	0.915	0.211	0.932	0.419
Ssa293	38	9	0.831	9.8	0.451	6.9	0.200	0.785	0.299	0.839	0.322
Ssa85	40	13	0.842	10.6	0.215	7.4	0.008	0.870	0.198	0.904	0.012
Ssa4	32	9	0.792	7.9	0.382	5.7	0.059	0.804	0.321	0.850	0.068
Wilmot Creek											
Omy325	52	17	0.905	16.8	0.531	12.1	0.046	0.899	0.463	0.926	0.076
Omy207	58	16	0.916	19.1	0.213	13.8	0.256	0.880	0.105	0.915	0.440
Ssa293	58	27	0.956	27.6	0.492	23.0	0.142	0.952	0.472	0.963	0.095
Ssa85	58	16	0.821	10.9	0.044	6.9	0.000	0.878	0.080	0.916	0.000
Ssa4	40	16	0.742	7.1	0.000	5.0	0.000	0.908	0.001	0.930	0.000
Shelter Valley											
Omy325	64	12	0.805	10.4	0.330	6.5	0.008	0.811	0.359	0.871	0.035
Omy207	62	15	0.913	19.2	0.125	13.6	0.354	0.864	0.048	0.905	0.399
Ssa293	58	23	0.955	27.4	0.132	22.8	0.535	0.935	0.041	0.952	0.324
Ssa85	58	21	0.887	15.6	0.056	10.6	0.000	0.923	0.081	0.944	0.000
Ssa4	48	19	0.769	8.2	0.000	5.5	0.000	0.920	0.000	0.940	0.000
Ganaraska River											
Omy325	52	14	0.861	12.8	0.397	8.6	0.016	0.862	0.381	0.901	0.059
Omy207	60	15	0.882	15.3	0.539	10.1	0.037	0.867	0.422	0.908	0.073
Ssa293	52	20	0.942	22.6	0.262	18.3	0.335	0.923	0.144	0.942	0.394
Ssa85	58	16	0.740	7.8	0.001	5.1	0.000	0.877	0.015	0.916	0.000
Ssa4	52	20	0.867	13.2	0.015	8.9	0.000	0.923	0.031	0.943	0.000

Note: H_o refers to unbiased heterozygosity (Nei 1987); k_o refers to the expected number of alleles according to Maruyama and Fuerst (1984). Pr (IAM) and Pr (SMM) refer to the probabilities that the number of alleles and heterozygosity values are as or more different from the values predicted by both models (for details, see Estoup et al. 1995). n = the number of genes surveyed.

Table 5. Estimates of effective population size and standard errors based on the IAM (Chakraborty and Neel 1989) for each of the populations and the mutation rates for each of the five loci investigated based on the assumption that the geometric mean of the mutation rates is 0.0001.

Sample site	Effective population size and SE
Salmon River	23 748±3189
Prince Brook	13 518±2409
Wilmot Creek	23 855±3422
Shelter Valley	21 445±3043
Ganaraska River	20 088±2931
Geometric mean	20 012
Locus	**Mutation rate ($\times 10^{-4}$) and SE**
Omy325	0.7730±0.1190
Omy207	0.8280±0.1230
Ssa293	1.3890±1.1920
Ssa85	1.0290±0.1470
Ssa4	1.0930±0.1650

and θ-based estimates, respectively). Although these values may be considered large from an evolutionary perspective (Carvalho and Hauser 1994), the estimate is small, from a management viewpoint, when compared with the geometric mean estimate of N_e, 7/20 012 = 0.03%. This suggests that on average, <<1% of any population is exchanged, although this estimate should only be considered a rough guide, as the assumptions on which it is based are not completely realistic.

Between-site heterogeneity was also investigated within regions, i.e., within New York and Ontario, and revealed a lower level of allele frequency heterogeneity, with only three of five loci (*Omy325*, *Omy207*, and *Ssa85*) demonstrating significance. A previous analysis of mtDNA variation among these populations demonstrated no population differentiation among all the Ontario populations studied, although the three Ontario populations did differ significantly from the two New York populations (Dueck 1994). The different heterogeneity estimates within Ontario between the marker sets are probably largely due to the differences in sample size, genetic variability, and stochastic events. This conclusion is supported by the

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Table 6. Values of f_i and associated probabilities for each locus at the five sites investigated.

Locus	Salmon River	Prince Brook	Ganaraska River	Wilmot Creek	Shelter Valley
Omy325	+0.142	+0.434***	+0.199*	+0.066	+0.148
Omy207	+0.073	–0.016	+0.247*	–0.055	+0.154**
Omy293	+0.021	+0.814***	+0.104*	+0.026	–0.011
Ssa85	+0.077	–0.009	+0.069	–0.051	–0.090
Ssa4	–0.081	+0.136**	+0.069***	+0.058	+0.190

Note: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

observation that only three of five microsatellite loci revealed significant allele frequency heterogeneity within Ontario. An alternative explanation could be sex-biased migration patterns with the female line primarily responsible for gene flow.

Genetic relationships

The topology of the trees generated from the microsatellite data (Fig. 2) was identical to the tree topology obtained from a previous mtDNA survey of these populations (Dueck and Danzmann 1996). The mtDNA-based tree, built using a Manhattan metric distance of haplotype frequencies, also revealed the Ganaraska population to be distinct from the Wilmot Creek/Shelter Valley grouping and intermediate to the New York populations. The relative dissimilarity of this site from the other two Ontario populations appears realistic, as the Ganaraska River has only been accessible to colonizing fish within the last 20 years after construction of a fish-way. Thus, this population has not experienced the same potential homogenizing effects of gene flow as the other two Ontario populations.

In summary, this study represents one of the first multiple microsatellite locus surveys of natural or self-sustaining populations of rainbow trout. The identification of five microsatellite loci in rainbow trout is described and primer sequences for seven salmonid microsatellite loci are included. High levels of variability were observed at all loci and this variation revealed significant differences among populations of rainbow trout within Lake Ontario. These data suggest that individuals are largely returning to specific river drainages to spawn and this has obvious implications for the management of the fishery. Tests of the SMM and IAM showed the predictions of the IAM to reflect more accurately the observed data.

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Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish

R.A. Myers, G. Mertz, and J. Bridson

Abstract: We examine the spatial scale of variability in recruitment for 11 marine, three anadromous, and five freshwater species. Generally the spatial scale of recruitment correlations for marine species is approximately 500 km, compared with less than 50 km for freshwater; anadromous species fall between these two scales. The scale for marine species is comparable with (but less than) that of the largest-scale environmental variables (and is compatible with the idea that large-scale environmental agents influence recruitment). Our results are consistent with the hypothesis that predation is a more important factor in determining recruitment in freshwater than it is in the marine environment.

Résumé : Nous avons examiné l'échelle spatiale de la variabilité du recrutement chez 11 espèces marines, trois espèces anadromes et cinq espèces d'eau douce. Généralement, l'échelle spatiale des corrélations de recrutement pour les espèces marines est d'environ 500 km, comparativement à moins de 50 km pour les espèces d'eau douce; pour les espèces anadromes, l'échelle se trouvent entre les deux. L'échelle des espèces marines est comparable (mais inférieure) à celle des variables environnementales de la plus grande échelle (et concorde avec l'idée que des agents environnementaux à grande échelle influent sur le recrutement). Nos résultats concordent avec l'hypothèse que la prédation est un facteur plus important pour la détermination du recrutement en eau douce que dans l'environnement marin.
[Traduit par la Rédaction]

Introduction

The sources of recruitment variability in fish populations have yet to be definitively identified (see Wooster and Bailey 1989 for a recent review). The relative importance of biotic factors (food supply, predation) and abiotic factors (temperature, stratification, currents, etc.) remains uncertain. The spatial scale of recruitment variability should furnish information as to the processes involved because different forcing agents will be characterized by different spatial scales (Koslow et al. 1987; Mann 1993). To date, the spatial scale for recruitment variability has been evaluated explicitly for only one species, Atlantic cod (*Gadus morhua*) (Myers et al. 1995*c*), and there has not been an attempt to compare the scales for marine, anadromous, and freshwater species. This paper addresses these issues by presenting an analysis of the spatial scale for recruitment variability for all species (marine, anadromous, and freshwater) for which sufficient data were obtainable. We attempt to draw conclusions about the relative weight of biotic and abiotic influences in freshwater and marine systems.

Methods and data

We assembled over 500 time series of spawner abundance and recruitment for fish populations (Myers et al. 1990, 1995b) (Fig. 1). The data are available from the first author in digital form.

The marine stocks included Atlantic cod, haddock (*Melanogrammus aeglefinus*), Atlantic herring (*Clupea harengus*), Pacific ocean perch (*Sebastes alutus*), plaice (*Pleuronectes platessa*), pollock (*Pollachius virens*), sole (*Solea vulgaris*), walleye pollock (*Theragra chalcogramma*), and whiting (*Merlangius merlangus*). We also considered all North Atlantic redfish of the genus *Sebastes* in one comparison and hakes of the genus (*Merluccius*) in another.

For most marine populations, spawning stock biomass (SSB) and recruitment were estimated by sequential population analysis (SPA) of commercial catch-at-age data. SPA techniques include virtual population analysis, cohort analysis, and related methods that reconstruct population size from catch-at-age data (Hilborn and Walters 1992). For six of the redfish populations, recruitment was estimated from research trawl surveys.

Three anadromous Pacific salmon species were studied: chum (*Oncorhynchus keta*), pink (*Oncorhynchus gorbuscha*), and sockeye salmon (*Oncorhynchus nerka*). For Pacific salmon stocks, spawner abundance is the estimate of the number of upstream migrants discounted for mortality within the river and recruitment combines catch and the number of upstream migrants. For pink salmon, we also used 10 time series of research estimates of eggs that overwinter and of the number of young fish (fry) that emerge from the gravel and migrate downstream to the ocean the following spring. For sockeye salmon, we had access to 11 studies in which there were estimates of egg or fry production and subsequent smolt production. These estimates do not rely on commercial catch data and avoid the difficulty of stock separation that plagues the analysis of commercial catch data. Obviously, they only analyze survival during the freshwater part of the life cycle.

The freshwater stocks included brook trout (*Salvelinus fontinalis*), northern pike (*Esox lucius*), sauger (*Stizostedion canadense*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*). The seven brook trout populations were from introduced populations in California mountain lakes (De Gisi 1994); these populations were estimated using research gill nets and maximum likelihood depletion estimation. Recruitment was estimated for the northern pike, sauger,

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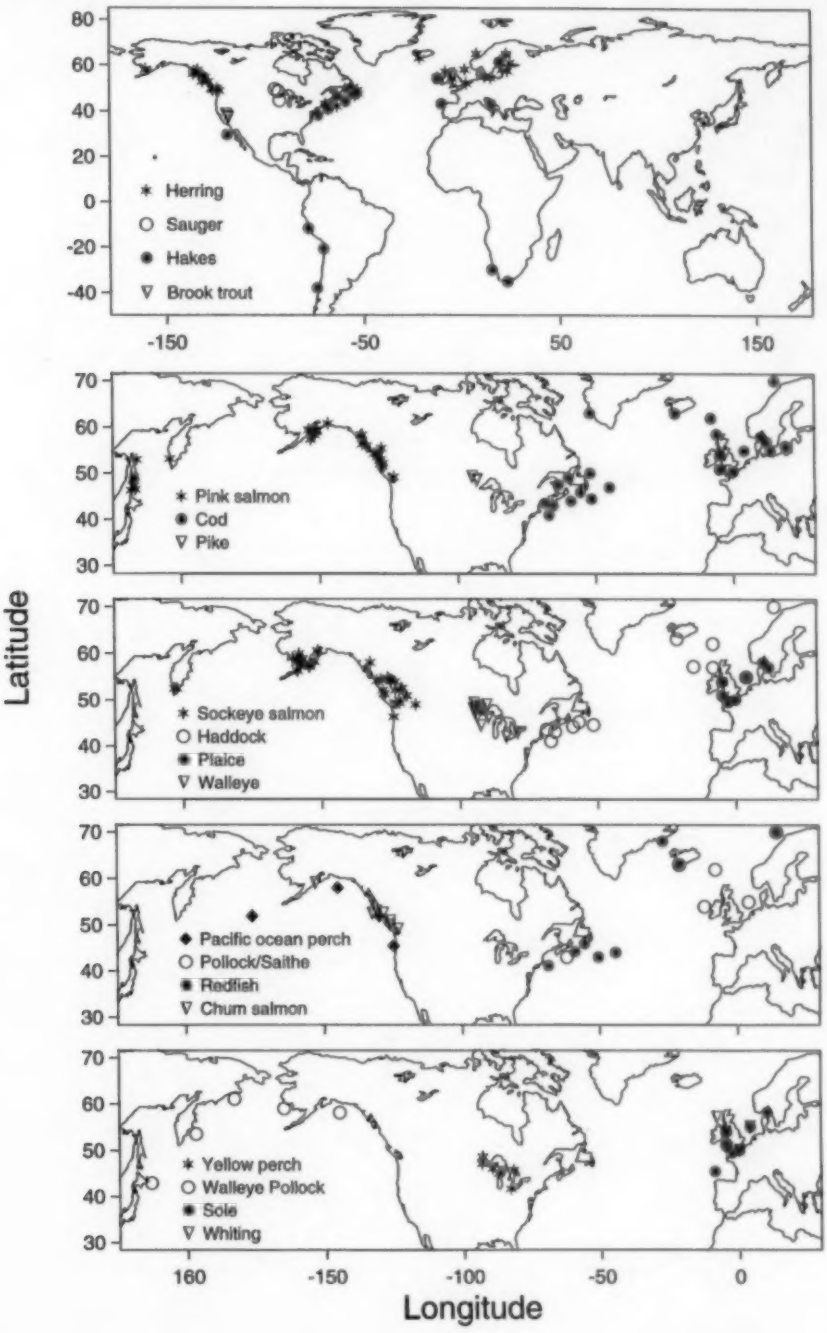
Fig. 1. Locations of populations used in the analysis.



and walleye by research gill nets, trawling, or SPA (for two walleye populations). Estimates of year-class strength were averaged over several ages for the research gill nets or trawls to minimize estimation error.

We fit a Ricker model (Hilborn and Walters 1992) to the recruitment, R, and spawner abundance estimates, S:

$$(1) \quad R = \alpha S e^{-\beta S}$$

The residuals from this regression were used to find the correlation between stocks. Other stock recruitment models, e.g., the Beverton–Holt (Hilborn and Walters 1992), were investigated and gave similar results. We also performed the correlation analysis for the logged

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Fig. 2. Correlation of recruitment between pairs of stocks, corrected for spawner abundance, versus distance between the stocks. Fits of the models $e^{-\frac{d}{v}}$ (solid curve) and $\rho_0 e^{-\frac{1}{2}\left(\frac{d}{\sigma}\right)^2}$ (broken curve).

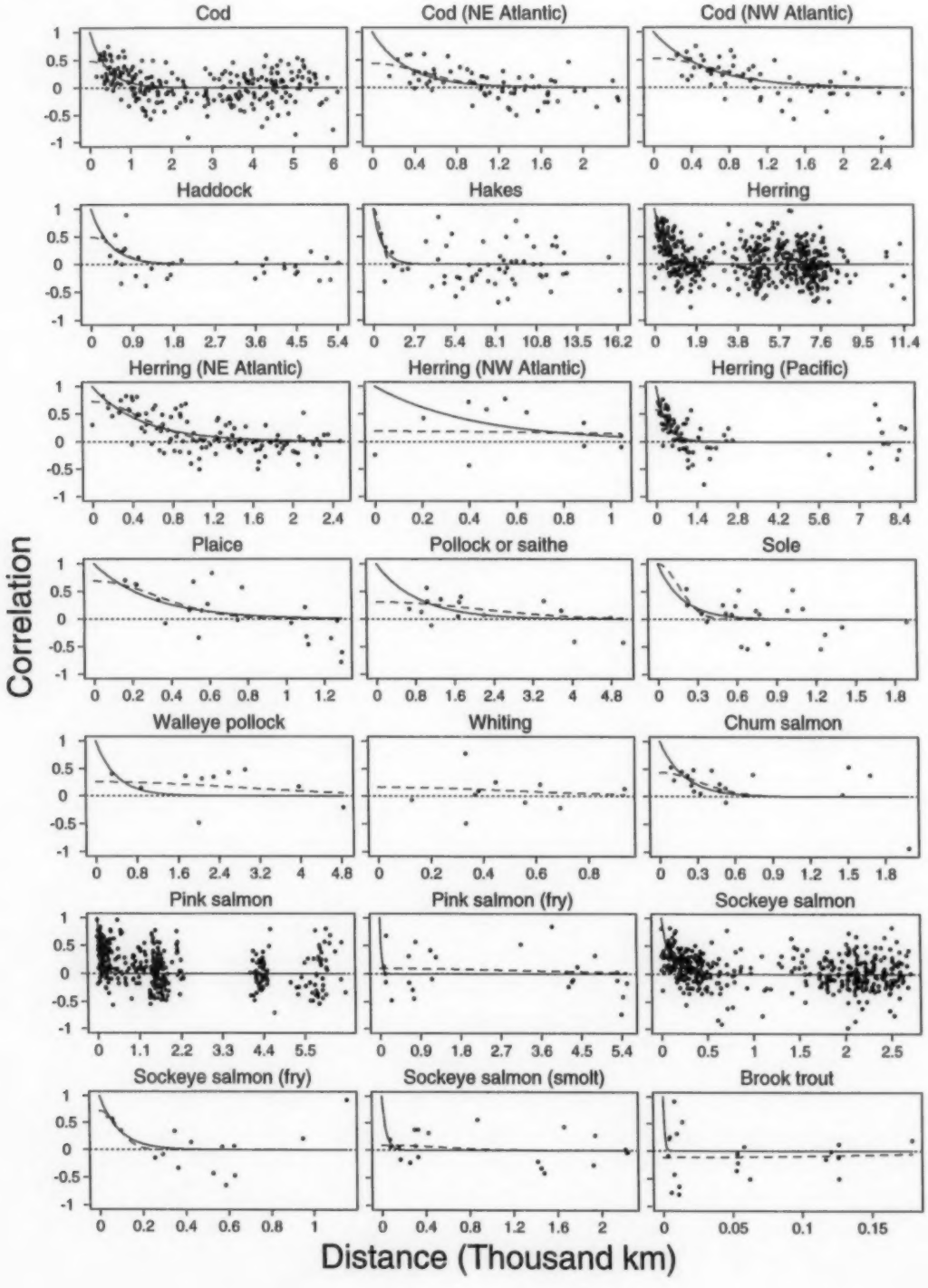

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Table 1. For each species the parameters for two different fits are given when using Ricker model residuals to determine correlation.

			$e^{-\frac{d}{\nu}}$		$\rho_1 e^{-\frac{1}{2}\left(\frac{d}{\sigma}\right)^2}$		
Species	n	df	ν	SS	ρ_1	σ	SS
Cod	23	252	420 (38)	8.8	0.49 (0.07)	570 (81)	8.6
NE Atlantic	12	65	330 (45)	2	0.44 (0.1)	500 (110)	1.9
NW Atlantic	11	54	540 (58)	1.5	0.53 (0.08)	680 (120)	1.4
Haddock	9	32	410 (98)	1.1	0.49 (0.28)	540 (220)	1.1
Hakes	12	57	590 (240)	2.8	1*	440 (110)	2.8
Herring	36	571	420 (32)	24	0.56 (0.05)	510 (51)	23
NE Atlantic	16	108	490 (48)	4	0.73 (0.08)	480 (53)	3.6
NW Atlantic	6	10	420 (280)	2.2	0.19 (0.21)	1300 (5000)	0.97
Pacific	14	84	340 (31)	2.3	0.57 (0.05)	430 (52)	2.1
Plaice	7	20	300 (100)	1.6	0.69 (0.3)	330 (140)	1.6
Pollock or saithe	6	14	860 (190)	0.51	0.31 (0.12)	2000 (1300)	0.41
Sole	7	20	180 (58)	0.9	1*	160 (30)	0.88
Walleye pollock	5	9	400 (270)	0.52	0.26 (0.19)	2800 (3100)	0.46
Whiting	5	9			0.16 (0.31)	510 (1300)	0.78
Chum salmon	7	18	200 (35)	0.51	0.44 (0.11)	320 (93)	0.46
Pink salmon	32	438	100 (7.6)	21	0.42 (0.03)	250 (37)	19
Egg to fry	10	25	32 (39)	1.3	0.09 (0.09)	3200 (5300)	1.3
Sockeye salmon	36	471	79 (6.1)	16	0.28 (0.03)	230 (27)	11
Egg to fry	9	14	90 (46)	0.71	0.72 (0.47)	82 (89)	0.7
Egg to smolt	11	19	38 (22)	0.57	0.09 (0.12)	520 (2100)	0.56
Brook trout	7	20	0.95 (3.5)	3.6	–0.11 (0.12)	150 (470)	3.4

Note: n gives the number of stocks, df gives the degrees of freedom for a one-parameter fit, ν is the parameter (with SE) for the exponential decay fit, and ρ_1 and σ (with SE) are the parameters for the Gaussian fit. The SS columns give the sum of squares for each model. An asterisk indicates whenever the constraint that ρ_1 be between 1 and –1 was invoked (reducing the second fit to a one-parameter fit). A unique estimate for the first model could not be found for whiting.

recruitment without adjustment for spawning biomass, which allows the inclusion of more stocks; the results were similar.

Estimating spatial scale

A simple estimate of the spatial scale is the distance over which the pairwise correlation between recruitment time series is reduced by a factor e^{-1}, i.e., the exponential decay rate or the e-folding scale. That is, we fit the model

$$(2) \qquad \rho(d) = \rho_0 e^{-\frac{d}{\nu}}$$

where ρ_0 is the correlation between two stocks at zero separation, ν is the e-folding scale, and d is the great circle distance between spawning locations of each population (kilometres). In this model, we constrain ρ_0 to have an absolute value of 1 or less. However, we also fit the model with ρ_0 constrained to be 1. We found that the model was rarely improved by estimating ρ_0; therefore, we will present only the results for ρ_0 constrained to be 1.

Some data sets appear to have a "shoulder" at $d = 0$; therefore, we fit the model

$$(3) \qquad \rho(d) = \rho_1 e^{-\frac{1}{2}\left(\frac{d}{\sigma}\right)^2}$$

where σ is the standard deviation of a normal distribution. These models were fit with nonlinear least squares weighted by the fraction of years for which the stocks had overlapping data. Pairs of stocks were only included if they had an overlap of at least 5 years.

Results

We initially fit the exponential model (eq. 2) with ρ_0 constrained to be 1 (Fig. 2; Table 1). The inclusion of the parameter ρ_0 in the model significantly improves the fit for only three species: haddock and pink and sockeye salmon (F-test; $p < 0.01$). These fits are not shown because they are very similar to the fits of eq. 3.

The fitting of eq. 3 to the data usually yields a correlation scale similar to that of the exponential fit. Exceptions occur when the correlation scale is small for the the exponential model, and the Gaussian model estimates a large σ and a small ρ_1, e.g., pink salmon egg to fry data. However, these estimates are never significantly different from zero and are best interpreted as showing that survival is essentially independent among populations. In some cases the "best" estimate of ρ_1 was greater than 1; in these cases, ρ_1 was constrained to be 1, which is noted by an asterisk in the tables.

The correlation scale was similar if we did not correct for spawner abundance (Table 2). For six species, there were insufficient data on spawner abundance, so the correlation scale is shown only for the unadjusted recruitment (Fig. 3).

For the marine species, the exponential fit with distance to the decay of the pairwise correlation of the residuals from the spawner recruitment function between all pairs of stocks shows that the e-folding scale is typically about 500 km (Fig. 2; Table 1).

The apparent positive correlation across the Atlantic for Atlantic cod was investigated by Myers et al. (1995*c*) and was found to be caused by long-term trends in the data. Plaice appear to be negatively correlated at the largest spatial scales; however, this relationship does not appear to be statistically significant.

For Atlantic herring, there are two notable outliers at a distance of zero for which the correlation is negative (Fig. 2).

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Table 2. Same as Table 1 except the effect of spawner abundance is not removed.

			$e^{-\frac{d}{v}}$		$\rho_1 e^{-\frac{1}{2}\left(\frac{d}{\sigma}\right)^2}$		
Species	n	df	v	SS	ρ_1	σ	SS
Cod	23	252	530 (53)	14	0.63 (0.09)	580 (79)	14
NE Atlantic	12	65	430 (64)	3.4	0.67 (0.15)	460 (91)	3.3
NW Atlantic	11	54	680 (82)	2.2	0.57 (0.09)	800 (150)	2.1
Haddock	14	83	500 (73)	2.9	0.56 (0.11)	600 (120)	2.9
Hakes	12	59	1000 (370)	3.5	0.88 (0.39)	780 (330)	3.4
Herring	42	782	480 (31)	38	0.63 (0.04)	520 (41)	36
NE Atlantic	16	108	490 (52)	5	0.63 (0.09)	530 (70)	4.8
NW Atlantic	12	65	650 (85)	4.7	0.65 (0.07)	660 (100)	4.3
Pacific	14	85	350 (40)	3.8	0.57 (0.06)	450 (65)	3.3
Pacific ocean perch	4	5	930 (250)	0.084	1*	750 (130)	0.068
Plaice	7	20	340 (120)	2.1	0.75 (0.3)	360 (140)	1.9
Pollock or saithe	6	14	970 (170)	0.43	0.61 (0.23)	1000 (320)	0.42
Redfish	8	24	670 (230)	1.7	0.38 (0.17)	1400 (810)	1.6
Sole	7	20	250 (49)	0.54	0.46 (0.17)	350 (110)	0.55
Walleye pollock	5	9	460 (310)	0.6	0.47 (0.41)	740 (830)	0.59
Whiting	5	9	210 (90)	0.59	0.44 (0.5)	280 (230)	0.56
Chum salmon	7	18	190 (47)	0.9	0.53 (0.17)	260 (89)	0.85
Pink salmon	32	439	140 (12)	31	0.51 (0.04)	230 (33)	29
Egg to fry	10	27	0.07 (0.12)	950 (3400)	1.3		
Sockeye salmon	36	476	180 (11)	20	0.47 (0.03)	290 (26)	18
Egg to fry	8	11	52 (28)	0.63	0.49 (0.46)	83 (130)	0.61
Egg to smolt	11	19	31 (28)	0.81	−0.09 (0.19)	240 (690)	0.81
Brook trout	7	20	3.6 (1.5)	2.4	0.17 (0.09)	240 (800)	2.1
Walleye	16	70	18 (9.1)	5.7	0.15 (0.1)	200 (180)	5.4
Pike	6	5	15 (10)	0.58	1*	11 (3.9)	0.44
Sauger	4	5	20 (11)	0.18	1*	14 (3.8)	0.18
Yellow perch	7	15	15 (9.1)	0.67	0.25 (0.23)	90 (120)	0.67

Note: A unique estimate for the first model could not be found for pink salmon in the fry stage.

These represent separate Atlantic herring stocks that spawn at different times of the year, i.e., spring- and summer-spawning Icelandic Atlantic herring and fall- and spring-spawning Atlantic herring in the Gulf of St. Lawrence. These populations will clearly be subject to different environmental forcings; we should not be surprised that they are different.

For pink and sockeye salmon during their freshwater life stages, there is very little spatial correlation in the interannual survival. The spatial scale of survival from spawner to recruit, with the inclusion of marine survival, is larger.

There are relatively less data for freshwater species; however, the pattern seen in the five species investigated is the same: the correlation scale is very small. For example, the correlation between brook trout populations is negative as often as it is positive (Fig. 3). This result is consistent with the small scale seen in the correlation of freshwater survival of pink and sockeye salmon.

Freshwater species, e.g., Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*), that spawn and live in the freshwater margins of the Baltic have spatial scales of recruitment larger than those that we have estimated for freshwater species (Böhling et al. 1991; Lehtonen and Lappalainen 1995). Larvae reared in the freshwater margins of the Baltic may be swept into the interior of this sea, so that these species, in effect, dwell in a marine environment.

Wind and thermal forcing of the ocean by the atmosphere may account for the large correlation scale for recruitment in marine systems. The site-to-site correlation of annual air temperature anomalies versus separation for maritime weather stations of the Northwest Atlantic is shown in Fig. 4; the Gaussian fit indicates that the correlation scale (σ) is 1100 km, with a standard error of 59 km (and with $\rho_1 = 0.905$, SE = 0.44). Sea surface temperature (SST) anomalies in the Northwest Atlantic have essentially the same correlation scale, about 1000 km (Thompson et al. 1988). This similarity is expected because SST variations are strongly influenced by thermal and wind forcing of the atmosphere (e.g., Thompson et al. 1988). Also shown in Fig. 4 (broken curve) is the Gaussian fit (Gunst 1995) to correlations of annual air temperature anomalies versus site separation for the continental United States. The correlation scale is similar to that for the marine sites, demonstrating that freshwater systems are exposed to climate signals having about the same scale as those influencing oceanic domains.

Discussion and conclusions

A simple generalization is apparent from our data: the correlation scale for recruitment of marine species is typically 500 km whereas for freshwater species, it is less than 50 km. This finding generalizes the conclusion of Myers et al. (1995*c*) who showed that the correlation scale for recruitment of Atlantic cod was about 500 km. Our result for freshwater is not consistent with claims that recruitment in walleye is synchronous over a wide spatial scale, i.e., approximately 1000 km (Colby

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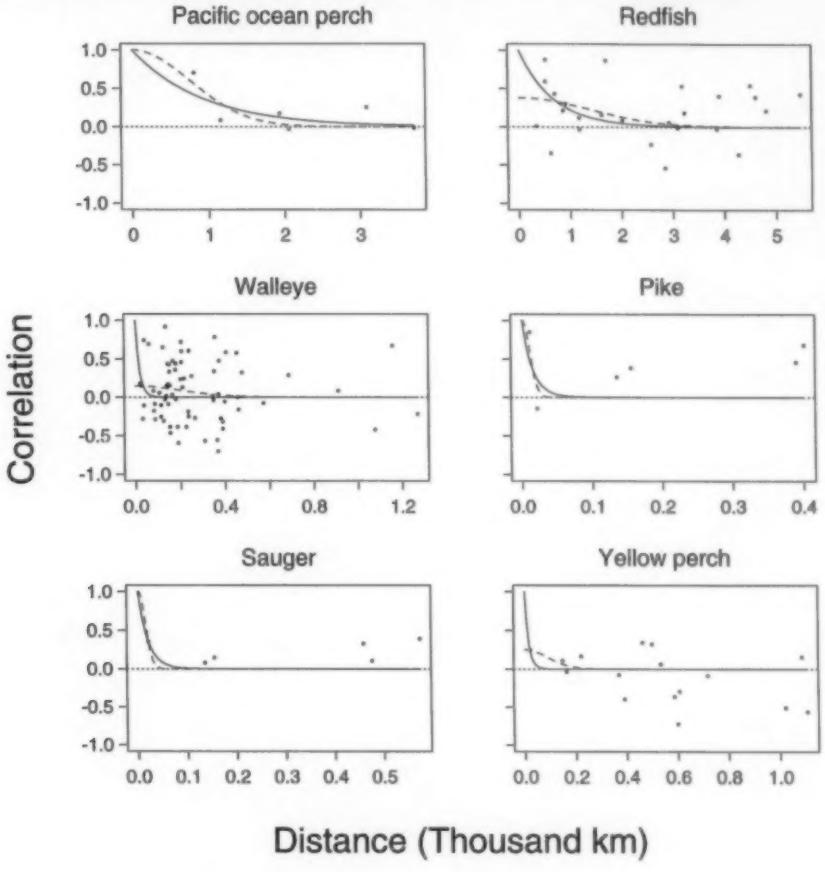
Fig. 3. Same as Fig. 2 for those species for which there were not sufficient data to correct for spawner abundance.



et al. 1979). The previous conclusion regarding walleye was based on the observation that the 1959 year-class was strong in many lakes, and not on a statistical analysis.

We have found no evidence of large-scale (thousands of kilometres) patterns of recruitment for any species, despite previous surmises of such patterns, particularly for Pacific sardine (*Sardinops sagax*) (Kawasaki 1992). We attempted to examine Kawasaki's intriguing hypothesis with recruitment data for Pacific sardine (Kawasaki used catch data). Although we located data for six Pacific sardine stocks, the degree of overlap was not sufficient to give reliable estimates. We hope that Kawasaki's hypothesis can be fully tested at a later time. The absence of convincing transocean-scale correlations is consistent with the findings of Myers et al. (1995*a*).

It is possible that transocean-scale correlations are present with a lag. The hypothesis of lagged correlations in recruitment across the North Atlantic was examined by Myers et al. (1995*a*) who found that new data did not support the previously published lagged correlations identified by Templeman (1972). Researchers who may be interested in this, or any other problem, may have access to our database.

We have chosen to summarize the correlations between recruitment time series in the simplest possible manner. However, there are species where a more detailed analysis is justified. For example, Myers et al. (1995*c*) separated the variability for Atlantic cod recruitment series into two components, low-frequency (periods greater than 10 years) and higher frequency variation, and demonstrated that the large-scale variability was seen only in the former. These larger scale correlations seen for Atlantic cod (see Fig. 1) appear to be caused by artifactal trends. An analysis separating the low-frequency and higher frequency variation may be important for some species. Again, our database is available to any researcher.

The existence of coherent recruitment fluctuations in marine systems on the order of 500 km suggests the influence of wind or SST because, in general, only these variables have sufficiently large correlation scales (about 1000 km) to account for the synchronous component of recruitment. Displacements of the edge of the Gulf Stream occur in unison over distances of 1000 km or more (Drinkwater et al. 1994) and could account for synchronous recruitment variations in the Northwest Atlantic (only). The possible role of wind effects is attested to by the study of Koslow et al. (1987). They showed that the second principal component of atmospheric pressure (representing a particular wind pattern) had an apparent significant influence on recruitment for Atlantic cod stocks from Greenland to Nova Scotia. Unfortunately, one cannot be certain

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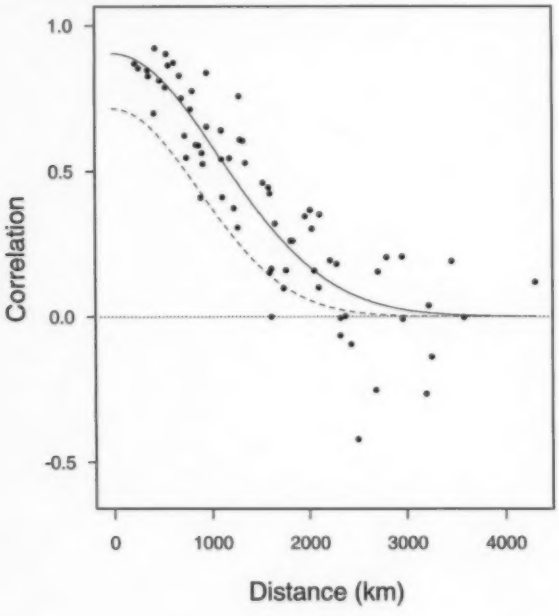
Fig. 4. Correlation of yearly air temperature anomalies between weather stations versus distance between stations (solid circles). Temperatures from maritime stations in the Northwest Atlantic from Godthaab, Greenland, to Cape Hatteras with over 50 years of data were used in the analysis (Drinkwater et al. 1994). We fit a Gaussian curve (solid curve) to the correlations as described in the text. We also plot (broken curve) the Gaussian fit, provided by Gunst (1995), to the correlation of annual U.S. air temperature anomalies (1951–1980) versus site separation. Note that different methods were used in the two analysis so that we do not claim that the two curves are different, only that the correlation scale in both cases is greater than 1000 km.



that this result is not an artifact of autocorrelation in the recruitment and environmental time series.

Lakes and streams are, like the oceans, exposed to very large-scale weather systems. For example, an advance or delay in vernal warming should cooccur at lakes separated by up to 1000 km (based on the correlation of air temperature anomalies in Fig. 4). Conceivably, these anomalies could affect the recruitment of spring-spawning species. On the other hand, lakes in quite close proximity to one another may exhibit unrelated patterns of temporal variation in certain chemical properties (Magnuson et al. 1990). Unfortunately, we cannot state with any certainty which variables are likely, in general, to exert the dominant influence.

As noted above, wind may impart large-scale synchrony to recruitment variations in marine systems. It is not clear that wind would have a similar effect in lakes. Small lakes may be sufficiently uniform that there are no unfavorable habitats into which the wind could drive eggs and larvae. (Fish stocks on oceanic shelfs are thought to suffer poor recruitment when eggs and larvae are exported to open ocean.) In shallow lakes, food supply for larvae may not change significantly when the wind mixes the water column, in contrast with the oceans, where wind mixing is thought to destroy the enhanced concentration of food at the pycnocline thought necessary to support some species of fish larvae (Lasker 1975).

An obvious difference between freshwater and oceanic systems is the size of the domains occupied by the fish stocks. The size factor may enter the picture when the influence of plankton patchiness on recruitment is considered. In oceanic regimes, eggs and larvae may be dispersed over a vast area, in effect averaging over a large number of patches. In contrast, in small lakes the recruitment variability associated with plankton patchiness may dominate (because there is little averaging over patches), thus masking large-scale influences.

Recruitment variability in freshwater may depend predominantly on biotic influences, particularly the predation by adults of one species on juveniles of another. Walleye predation has been shown to have a significant impact on year-class strength of yellow perch in Oneida Lake (Mills et al. 1987). In contrast, these effects have not been convincingly demonstrated in marine systems (Leggett and DeBlois 1994). Verity and Smetacek (1996) have conjectured that predation is a less dominant influence in marine systems because fish densities appear to be 10–1000 times smaller than in freshwater systems (Horn 1972).

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Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) in late summer: evidence of diel activity partitioning

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Abstract: Paired day–night underwater counts of juvenile Atlantic salmon (*Salmo salar*) were completed on tributaries of the West River, Vermont, U.S.A., between 28 August and 10 September 1995. At water temperatures ranging from 13 to 23°C, the relative count of juvenile salmon was greater at night. Nocturnal counts differed for young-of-the-year and post-young-of-the-year (PYOY) salmon, with PYOY exhibiting almost exclusive nocturnal activity. Nocturnal activity in late summer may enable salmon to maintain population densities when space and suitable feeding areas may be limited. Nocturnal activity of juvenile salmon should be considered in studies of habitat use, competition, time budgets, and associated bioenergetic processes.

Résumé : Des dénombrements appariés jour-nuit du saumon atlantique (*Salmo salar*) ont été réalisés dans les tributaires de la rivière West, au Vermont, É.-U., entre le 28 août et le 10 septembre 1995. À des températures de l'eau variant de 13 à 23°C, le dénombrement relatif de saumons juvéniles était plus élevé la nuit. Les dénombrements nocturnes ont différé pour les saumons qui sont des jeunes de l'année et les saumons qui ne sont plus des jeunes de l'année, ces derniers montrant une activité presque exclusivement nocturne. L'activité nocturne à la fin de l'été peut permettre au saumon de maintenir des densités de population lorsque l'espace et les aires d'alimentation convenables sont limités. L'activité nocturne du saumon juvénile devrait être prise en considération dans les études sur l'utilisation de l'habitat, la compétition, l'emploi du temps et les processus bioénergétiques connexes.
[Traduit par la Rédaction]

Introduction

Nocturnal activity of juvenile Atlantic salmon (*Salmo salar*) is a temperature-dependent behavior involving in part an increase in nighttime feeding at decreasing laboratory water temperatures (Fraser et al. 1993). Laboratory and field analyses further confirmed that nocturnal activity is controlled by water temperature rather than photoperiod or a predetermined circannual rhythm (Fraser et al. 1995), as suggested by Rimmer et al. (1983, 1984). Fraser et al. (1995) found that juvenile salmon increase their daytime occupation of shelters with decreasing water temperatures but remain nocturnally active at laboratory water temperatures ranging from 2 to 18.5°C.

While Fraser et al. (1995) provided evidence for a temperature-dependent basis of diel activity patterns, several points warrant further consideration. All field work in their study was completed at water temperatures ≤ 8.4°C; therefore, patterns of day and nighttime activity that they observed in the laboratory at water temperatures ranging from 9 to 18°C may not apply in the wild. In addition, young-of-the-year (YOY) salmon were used in their laboratory experiment, yet older juvenile salmon (parr) from three seasonal periods (April, June, October) were described in the field analysis; no distinction was made between the diel activity patterns of these life stages. Although juvenile Atlantic salmon have been observed to be active at night in the winter (Fraser et al. 1993), summer nocturnal activity at seasonal water temperatures in the natural environment has not been documented. Our objectives were to determine the level of nocturnal activity of juvenile Atlantic salmon and if YOY and post-young-of-the-year (PYOY) salmon exhibit similar diel activity patterns in the wild during late summer.

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Materials and methods

Study area and species

Underwater surveys were completed in tributaries of the West River, Vermont: Rock River, Marlboro Branch, Wardsboro Branch, and Utley and Greendale brooks (43°08′N, 73°25′W; Fig. 1). The West River is a tributary of the Connecticut River. Eight survey sites were selected on the five study streams (Fig. 1). Discharge (cubic metres per second) determined on 7 September 1995 in each tributary was 0.19 for the Rock–Marlboro system, 0.094 for Wardsboro, 0.088 for Utley, and 0.042 for Greendale. Water depth was recorded at 0.5-m intervals across transects spaced 4 m apart at each survey site on 6 September 1995. Maximum water depth along each transect was also determined and the mean maximum water depth for each survey site was calculated for comparison purposes (Table 1).

Juvenile salmon in the study streams originated from annual

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Fig. 1. Location of survey sites in the West River Basin, Vermont. The Connecticut River Basin is shaded.

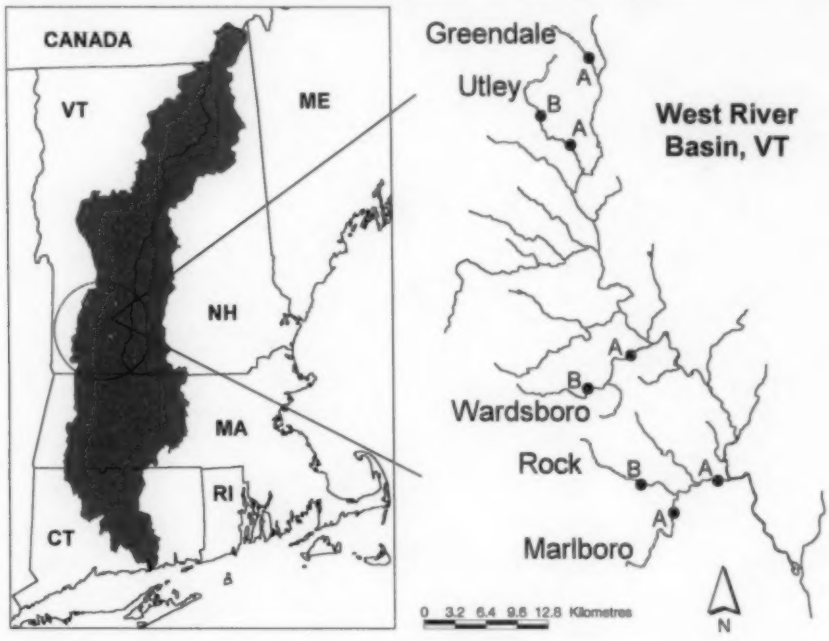

Table 1. Number of paired day–night snorkeling surveys completed and mean (±1 SE) physical characteristics of the survey sites (see Fig. 1 for location of survey sites).

Stream	Survey site	Number of paired snorkeling surveys	Mean water depth (cm)	Mean maximum water depth (cm)	Mean width (m)	Length (m)
Rock River	A	3	14.8 (0.9)	27.6 (0.9)	5.01 (0.35)	33.4
Rock River	B	3	18.6 (1.1)	34.7 (0.9)	9.41 (0.50)	32.3
Marlboro Branch	A	3	14.2 (0.8)	23.2 (0.4)	6.67 (0.33)	22.0
Wardsboro Branch	A	1	17.9 (1.2)	28.5 (1.1)	7.18 (0.33)	42.0
Wardsboro Branch	B	1	14.6 (0.7)	25.2 (0.6)	8.02 (0.55)	28.0
Utley Brook	A	1	18.2 (1.3)	27.1 (0.8)	5.99 (0.31)	32.0
Utley Brook	B	1	10.5 (0.7)	21.2 (0.4)	8.89 (0.28)	32.0
Greendale Brook	A	3	7.9 (0.4)	14.6 (0.2)	6.01 (0.44)	45.0

stockings of unfed fry during April and May at target densities of 30–50·100 m^{-2}. Although stocking densities in individual tributaries differ, they generally result in yearling parr densities of 6·100 m^{-2} (McMenemy 1995). Most juvenile salmon spend two winters in these tributaries before migrating as smolts (K.G. Whalen and D.L. Parrish, unpublished data). Several adult salmon have been observed in the West River system, but the extent of natural spawning is assumed to be minimal. Other species commonly encountered in the study streams included brook trout (*Salvelinus fontinalis*), longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), white sucker (*Catostomus commersoni*), and slimy sculpin (*Cottus cognatus*).

Snorkeling observations

We used snorkeling observations to quantify the number of YOY and PYOY juvenile Atlantic salmon holding position on or above the substrate during the day and night at the eight survey sites. We could not visit all sites on the same day or visit all sites the same number of times (Table 1) during the 28 August to 10 September 1995 survey period. Sampling throughout the study period was performed by two snorkelers, with each snorkeler surveying individual sites. Each site was always sampled by the same individual to reduce observational bias (Hankin and Reeves 1988). In addition to Atlantic salmon, the number of brook trout, white sucker, slimy sculpin, and longnose dace holding position on or above the substrate was also quantified; blacknose dace were too numerous to count accurately. The survey procedure was as follows. The snorkeler entered the water downstream of the survey site and moved upstream while searching for and counting all target species holding position on or above the substrate. The survey course included both midstream and peripheral habitats. YOY and PYOY salmon were readily distinguishable based on size (YOY < 90 mm TL, PYOY > 110 mm TL; K.G. Whalen and D.L. Parrish, unpublished data), as were brook trout and white sucker. Search time was directed at enumeration, not behavioral observations. Because water depth limitations precluded our ability to search the entire wetted area of each survey site and a significant difference in time spent on snorkeling observations between day and night surveys was detected (Wilcoxon paired-sample test; mean difference ± 1 SE = 3.4 ± 1.1 min; night > day; $p = 0.009$), we adjusted snorkeling counts relative to the time spent searching (i.e., relative count = total number of fish observed per minute spent snorkeling). To compare patterns of diel activity among YOY and PYOY Atlantic salmon and

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between other species, we standardized relative count data by calculating a nocturnal index (Fraser et al. 1995):

$$\text{Nocturnal index} = 100 \times \frac{RC_n}{RC_n + RC_d}$$

where RC_n = night relative count and RC_d = day relative count.

Water temperature was recorded at the beginning of each survey with a hand-held thermometer. Only trace precipitation (<1 cm) occurred during the study period. Underwater visibility was a minimum of 3 m on each sampling occasion, with vision being more commonly obstructed by underwater structure than water clarity. All sampling was performed during relatively cloudless days and nights. All surveys were completed between 13:30 and 00:30. Night surveys were performed with the aid of an underwater hand-held white light. We minimized fish displacement by directing the light beam at the underside of the water surface (Contor and Griffith 1995). During the survey period, sunrise occurred between 05:08 and 05:23 and sunset occurred between 18:11 and 18:34. Darkness generally occurred approximately 45 min after sunset (i.e., 19:00). Day and night observations at each survey site were paired; both observations were completed during the same 24-h period. The total underwater search time for the survey period was 12.9 h (day = 6.0 h and night = 6.9 h).

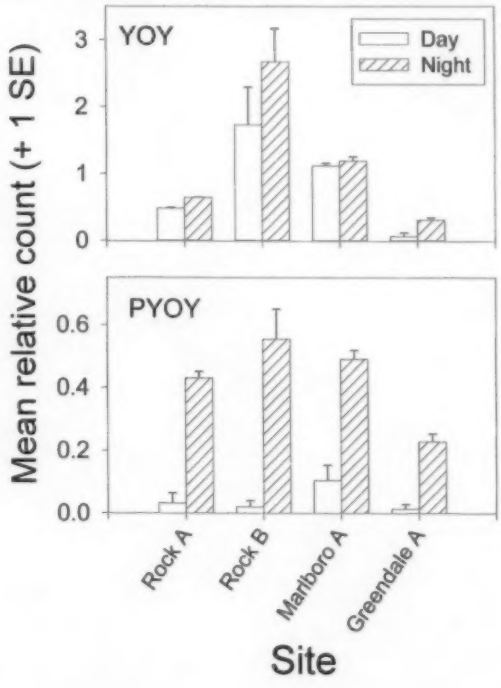
Statistical analyses

Two approaches were used in the analysis of the salmon data: (*i*) day and night comparisons, for which we defined discrete time periods of 13:00–17:00 for day and 20:15–23:30 for night, and (*ii*) hour of the day analysis, for which we treated the hour of the day the sample was taken as a continuous measure that encompassed the entire range of times (13:30–00:30) when surveys were completed. Using these two approaches allowed us to compare day and night relative counts and also to examine how relative counts changed over time. Data from all eight survey sites were included in the hour of the day analysis, while data from the four survey sites visited on three occasions were used for day and night comparisons (Table 1).

To compare day and night relative counts of YOY and PYOY juvenile Atlantic salmon, we used a three-factor repeated measures analysis of variance (ANOVA; Cody and Smith 1991). The ANOVA was blocked by survey site with repeated measures on both phase (day, night) and sample date (early, middle, late). This approach enabled us to account for variation associated with the survey site, which was significant, yet maintain pairing in the day and night samples as well as balance in the design. A logarithmic transformation ($\ln(x + 1)$) was applied to the YOY and PYOY salmon relative count data to meet the assumptions of the repeated measures ANOVA (Neter et al. 1990). Statistical tests reported for the YOY and PYOY salmon relative count data are from transformed data, but means and cumulative percentages reported in the text and figures are pretransformed. To compare the nocturnal index of YOY and PYOY salmon, we used the same approach and design as above but with stage (YOY, PYOY) replacing phase in the analysis. As before, only the nocturnal index values calculated from relative count data collected from 13:30 to 17:00 and from 20:15 to 23:30 were used in the analysis. We evaluated the influence of daytime water temperature on nocturnal activity by plotting the nocturnal index of YOY and PYOY salmon and daytime water temperature. Nocturnal index values for this relationship were calculated using relative count measures from the discrete periods of the day and night.

For hour of the day comparisons between YOY and PYOY salmon, we computed a weighted hourly relative count index based on the division of the total count of salmon, either YOY or PYOY, by the total time spent searching over all sites in the respective hour of the day. Sampling was conducted during every hour of the day between 13:30 and 00:30 except 16:00 (±0.5 h). We then calculated a cumulative relative count measure to facilitate comparisons in the diel relative count pattern between YOY and PYOY salmon. All statistical tests were performed using SAS (SAS 1988). Significance of tests was determined at the 0.05 α level.

Fig. 2. Day and night mean relative counts of YOY and PYOY juvenile Atlantic salmon at survey sites visited on three occasions.



Results

During the survey period, 212 juvenile Atlantic salmon were observed during the day and 534 were observed at night. Marginal differences in relative counts between day and night were found for YOY salmon ($p = 0.08$) and large differences for PYOY salmon ($p = 0.007$) at water temperatures ranging from 13 to 23°C. Relative counts at all sites were greater at night for both YOY and PYOY salmon (mean difference ± 1 SE: YOY = 0.35 ± 0.12, PYOY = 0.38 ± 0.04; Fig. 2).

From 13:00 to 19:00, YOY salmon were much more abundant than PYOY salmon, which was followed by a threshold-like increase in cumulative relative counts for both YOY and PYOY salmon as darkness progressed (>19:00; Fig. 3).

The nocturnal index of PYOY salmon was consistently larger than that for YOY salmon at all sites ($p = 0.021$; mean difference ± 1 SE: 28 ± 4%; Fig. 4). PYOY salmon were almost exclusively nocturnal, while YOY salmon became increasingly nocturnal at lower daytime water temperatures (Fig. 5). Thus, as daytime water temperature decreased, so did the disparity between the nocturnal index of YOY and PYOY salmon.

All other species observed were active both diurnally and nocturnally. Data for these species were collected between 13:30 and 00:30 (±0.5 h), with 19:00 as the demarcation between day and night. The nocturnal index, pooled over all survey sites, was 61% for slimy sculpin ($n = 59$), 80% for longnose dace ($n = 91$), 52% for white sucker ($n = 43$), and

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Fig. 3. Cumulative percent of relative counts of YOY and PYOY juvenile Atlantic salmon by hour of the day sampled using relative count data pooled over all survey sites. No observations were made at 16:00 (±0.5 h). Darkness occurred after 19:00.

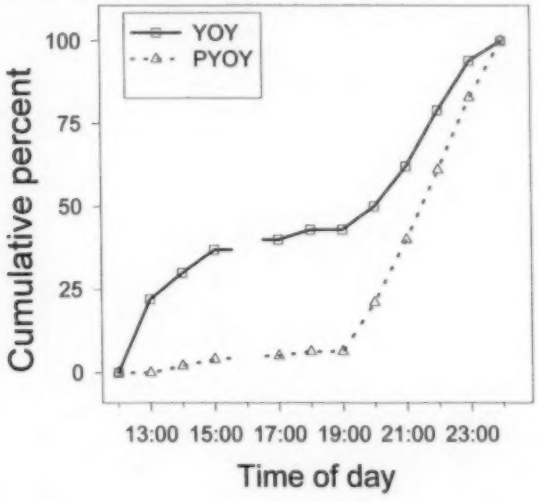
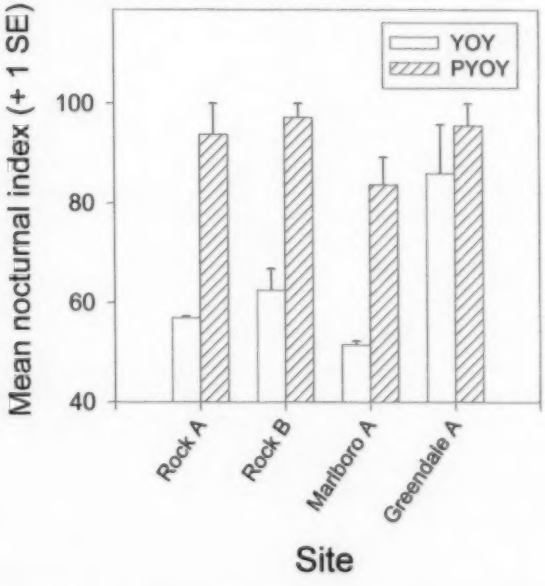


Fig. 4. Mean nocturnal index of YOY and PYOY juvenile Atlantic salmon at survey sites visited on three occasions.



84% for brook trout ($n = 14$). YOY white sucker and brook trout were observed during both day and night, yet PYOY white sucker and brook trout were only seen at night.

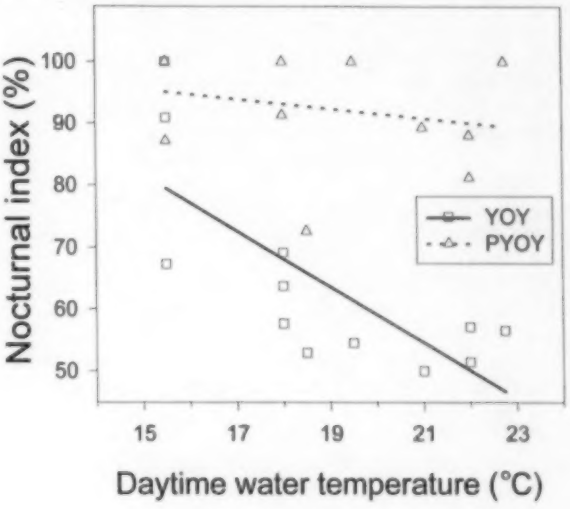
Discussion

We observed differences in the relative counts of YOY and PYOY juvenile Atlantic salmon between day and night during underwater surveys at water temperatures ranging from 13 to 23°C, which extends observations above the maximum of 8.4°C previously assessed in the natural environment (Fraser et al. 1995). Our results indicate that YOY salmon daytime relative count continuously decreases with declining daytime water temperatures without an apparent threshold effect. Moreover, the diel relative counts of YOY and PYOY salmon were skewed towards nocturnal activity at water temperatures where Fraser et al. (1995) observed equal daytime activity. This suggests that within certain seasonal periods and water temperature ranges, other factors in addition to water temperature may interact to determine diel patterns of activity.

Differences in the pattern of the nocturnal index of YOY and PYOY salmon were found, with PYOY salmon exhibiting almost exclusive nocturnal activity during the survey period. Unlike YOY salmon, most male PYOY salmon in our system in late summer mature in the fall, undergo a parr–smolt transformation in the spring, or both (K.G. Whalen and D.L. Parrish, unpublished data). Because differences in life stage influence other behaviors of juvenile Atlantic salmon in the fall (e.g., feeding; Huntingford et al. 1988; Metcalfe et al. 1988), it is not surprising that the diel activity of YOY and PYOY salmon differed. In addition to juvenile Atlantic salmon, we observed differences in the day and night relative counts of YOY and PYOY brook trout and white sucker. For each of these species, PYOY were observed almost exclusively at night, while YOY were observed during both day and night. We term this allocation of a fish's activity to either the day or night as diel activity partitioning (DAP). The similar pattern of DAP we observed for these three species indicates that this phenomenon is not exclusively an anadromous life history feature and may be unrelated to salmon life history.

Nocturnal activity has been associated with predation risk in both temperate freshwater stream (Culp 1989) and lake (Emery 1973; Helfman 1981; Hanych et al. 1983) fish. DAP where larger individuals are primarily nocturnal has been

Fig. 5. Relationship between daytime water temperature and the nocturnal index of YOY and PYOY juvenile Atlantic salmon. Regression lines are drawn to help present general trends. $n = 12$ for both YOY and PYOY salmon.



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observed in temperate freshwater lake fish (Helfman 1981; Magnan and FitzGerald 1984), where it has been suggested to be related to the greater predation risk for larger individuals during the day (Cerri 1983). Similarly, under increasing predation risk, larger baetid mayflies become increasingly nocturnal (Allan 1978; Culp and Scrimgeour 1993). Because diel activity patterns are influenced by water temperature (this study; Fraser et al. 1993, 1995) and potentially affected by seasonal and diel patterns of food availability and feeding motivation (Allen 1940; Wankowski 1981; Metcalfe et al. 1986, 1988; Adams et al. 1988), predation risk must be considered within a larger context of factors that may affect diel activity. Predation risk as the cause of nocturnal activity will therefore require further evaluation and careful consideration of potentially important interacting factors.

Hypotheses for why juvenile Atlantic salmon evolved certain patterns of diel activity are limited by the range of data from which they are formulated. For juvenile Atlantic salmon, daytime selection of substrate shelters in autumn (Rimmer et al. 1983) and winter (Cunjak 1988) has been suggested to be a response to a reduction in swimming performance at low water temperatures (Rimmer et al. 1985). The nighttime emergence of juvenile salmon at low water temperatures to feed (Fraser et al. 1993) was hypothesized to be a behavioral response to increased daytime predation risk because of temperature-induced energetic constraints, as well as to nightly patterns of ice formation (Heggenes et al. 1993). Our findings of nocturnal activity at high water temperatures, in conjunction with concordant results from the laboratory (Fraser et al. 1995), indicate that nocturnal activity is not exclusively a winter behavior and occurs when these fish are likely not energetically constrained or affected by ice formation.

Our study was limited to a short seasonal period and results should be interpreted within the context of a potential late summer, low flow, high water temperature interaction. Further analysis of juvenile Atlantic salmon diel activity patterns over a broader seasonal period and diversity of stream habitats would be prudent. Because we found nocturnal activity to represent a significant component of the diel activity pattern of juvenile Atlantic salmon, nighttime behavior should be considered in studies of competition, habitat use, self-thinning, time budgets, and associated bioenergetic processes.

Juvenile Atlantic salmon share the riverine environment with fish known to exhibit nocturnal behavior in summer (Cerri 1983; Fraser and Emmons 1984; Reebs et al. 1995) and we found nocturnal activity to be a community-wide phenomenon for the assemblage of stream fish we analyzed. We also observed trends in day and night activity similar to those reported in other regions of North America for longnose dace (Culp 1989) and white sucker (Campbell 1971; Emery 1973; Reebs et al. 1995). That nocturnal activity is both commonly exhibited and broadly distributed suggests that it is important to stream fish communities and therefore should be addressed at a community level. Understanding the evolution and importance of nocturnal activity in juvenile Atlantic salmon will probably be enhanced by assessing nocturnal behavior in other geographical areas and by continuing to address salmon behavior within the context of the entire fish community.

Diel abundance patterns may be critical to population regulation in stream salmonids (Fraser et al. 1995). Population density of stream salmonids is thought to be limited by territory size (Chapman 1966; Allen 1969; Grant and Kramer 1990) where territories are defended from intruders by agonistic behaviors (Kalleberg 1958; Keenleyside and Yamamoto 1962; Hartman 1965). We noted, however, that juvenile salmon at night seemed docile and tolerant of neighboring conspecifics, as has been observed under winter conditions for Atlantic salmon in the laboratory (Fraser et al. 1993) and for the closely related brown trout (*Salmo trutta*) in the wild (Heggenes et al. 1993). Because juvenile salmon appear tolerant of conspecifics at night, far higher densities may be maintained through nocturnal activity than would be possible with strict diurnal activity. Thus, nocturnal activity may be a response that enables these fish to maintain population densities during a period of the year when space and suitable feeding areas are limited. In this regard, the observed DAP among YOY and PYOY salmon may also prove to be advantageous by enabling YOY salmon access to resources and feeding opportunities that may otherwise be suppressed in the presence of PYOY salmon.

The consistency in night relative counts of PYOY Atlantic salmon that we observed may have practical applicability for management purposes because of the importance of indexing in their population assessment (Crozier and Kennedy 1995). Cunjak et al. (1988) assessed the reliability of underwater observations to estimate juvenile Atlantic salmon abundance by completing daytime (08:30–15:00) snorkeling and electrofishing surveys in late summer at high water temperatures (15–20°C). Generally poor agreement was found between visual and electrofishing estimates of juvenile salmon abundance (Cunjak et al. 1988). This difference was attributed to the habitat preference of young salmon and to the heterogeneity of surveyed habitats. Based on our results, the disparity that Cunjak et al. (1988) observed may also have been related to late summer patterns of nocturnal activity. Our data suggest that visual estimation via night snorkeling may be a useful technique for estimating the abundance of juvenile Atlantic salmon, especially in areas that are difficult to sample using a traditional method such as electrofishing or when minimal fish disturbance is a goal.

Acknowledgments

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A recruitment index and population model for spiny lobster (*Panulirus argus*) using catch and effort data

Paul A.H. Medley and Christopher H. Ninnes

Abstract: Using only catch numbers and effort data, we developed a recruitment index that exploits underlying seasonal changes in lobster size frequencies in the Turks and Caicos Islands' spiny lobster (*Panulirus argus*) fishery. The recruitment index was successfully used to model the lobster population dynamics. An empirical bootstrap method to simulate observation errors suggests that the models are robust enough to form the basis of a management plan. A tentative stock–recruitment relationship between estimates of the spawning stock and recruitment has been identified that can be used to guide escapement levels from the fishery. If correct, the stock–recruitment relationship indicates that the lobster population is largely self-recruiting.

Résumé : En utilisant seulement les données sur les prises et l'effort, nous avons élaboré un indice de recrutement qui exploite les variations saisonnières inhérentes des fréquences de taille des langoustes dans la pêcherie de langoustes (*Panulirus argus*) des îles Turks et Caicos. L'indice de recrutement a été utilisé avec succès pour modéliser la dynamique des populations de langouste. Une méthode empirique de bootstrap pour simuler les erreurs d'observation indique que les modèles sont suffisamment robustes pour former la base d'un plan de gestion. On a déterminé une relation stock–recrutement provisoire entre les valeurs estimées du stock de reproducteurs et du recrutement qui peut servir de guide pour déterminer les degrés d'échappement de la pêcherie. Si elle est correcte, la relation stock–recrutement indique que la population de langoustes dépend en grande partie de l'auto-recrutement.
[Traduit par la Rédaction]

Introduction

In spiny lobster (*Panulirus argus*) fisheries annual catches depend upon highly variable recruitment (Cobb and Phillips 1994). This presents a problem when the only information available is catch and effort, with little or no size frequency data. Although larval settlement or recruitment can be measured directly, it is likely that a time series of at least 10 years would be required before such an index can be used reliably for forecasting (Phillips et al. 1994).

Abundance indices for juvenile lobsters, derived from postlarvae collectors or from sampling prefishery recruits, have been successfully used in predicting future catches (Caputi and Brown 1986; Phillips 1986; Phillips et al. 1994). Catch and effort data, when size frequency data are available from recruits and prerecruits, have been used to predict the abundance of larger lobsters from smaller size-classes (Gonzalez-Cano 1991). These results suggest that an abundance index of young lobsters could provide the basis of a population model.

Turks and Caicos lobster fishery

Fishery

The Turks and Caicos Islands are at the southern end of the Bahamian archipelago in the Atlantic Ocean. Commercial fishing is based on the larger of three areas of shallow water, the Caicos Bank, which has an area of 6500 km^2. The catch is dominated by spiny lobsters during the lobster season (August–March) and conch (*Strombus gigas*) during the closed season.

Fishers generally leave around 07:00 and return to land their catch by 16:00 each day. Each boat carries one to three fishers, and the larger crews often have a nondiving boat driver. Depending on their capability, fishers can dive down to 30 m using only mask, fins, and snorkel, although the majority work in water 3–20 m deep.

The lobsters are caught from within their dens where they aggregate during the day. Fishing is largely limited to lobster dens that can be located from the surface, usually patch reefs. However, there are an unknown number of caves and holes in the limestone that cannot be seen from above water. These, together with deeper water habitat, act as a refuge for the lobster population.

Lobsters are mainly caught by impaling them on a fish hook that is attached to the end of a short fibreglass rod. Before 1982 the hook was illegal and the predominant gear used was the toss, which is a wire noose attached to the end of a pole. This was slipped around the tail of the lobster and pulled tight, allowing the capture of only one lobster per dive. Legalizing the hook decreased the time spent catching lobsters once they were found. Trapping only accounts for 5–10% of the total catch.

Data sources

Catches of lobsters are recorded as pounds landed by each boat at the end of each day's fishing at one of the processing plants,

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Fig. 1. Lobster size frequencies from the five main fishing grounds. Size increases from the shallow-water sites, the Bank (*a*, 3–6 m depth), and North Ambergris/the Lake (*b*, 4–12 m depth) through the southern cays (*c*, 6–12 m depth) to grounds on the edge of the bank, Bush Cay (*d*, 12–20 m depth), and East Side (*e*, 12–20 m depth), where most berried females are found.

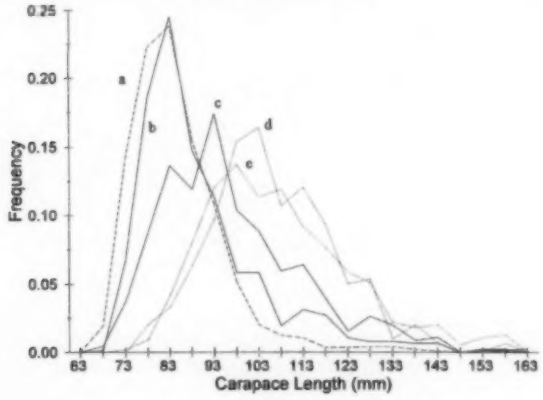
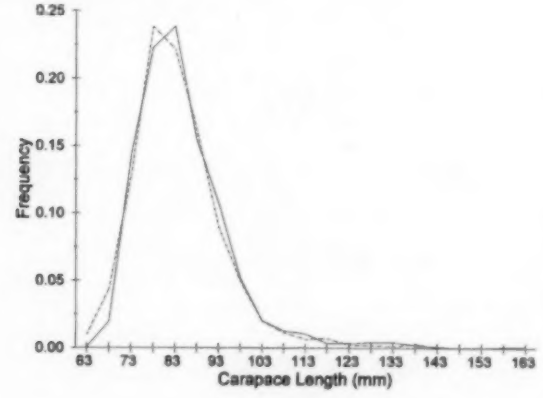


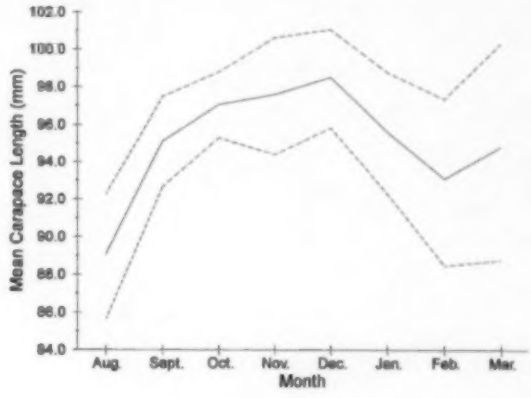
Fig. 2. Size frequency of August catches (broken line) for comparison with catches from the main shallow-water fishing ground, the Bank (solid line). August catches are predominantly derived from shallow sites harbouring small lobsters, which are new recruits to the fishery.



of which there are presently five. Lobsters are landed whole, and the principal exports are frozen tails. Daily landings and effort (boat days) are available for 1977– 1995, with the exception of the 1984 and 1985 seasons when effort data were not collected. Summary total landings for each month also exist for 1966, when the lobster fishery expansion began.

Exports classified by tail weight exist for the periods 1974–1983 and 1989 onwards. These incomplete size frequency data were used to convert mass to numbers landed. For the missing years the average size has been estimated from the mean size for the preceding and succeeding years. In addition, landings have been sampled since 1989, recording details of the fishing trip, such as the fishing ground, as well as taking measurements from the catch, including the carapace length and the presence of a spermatophore (tar spot) on female

Fig. 3. Mean (solid line) and standard deviation (broken lines) of lobster sizes caught in each month, estimated from export tail-weight size-classes (1974–1995). The standard deviation indicates the between-year variation in mean size. The mean August sizes are probably biased (see Fig. 2), as all lobsters below the minimum size (83 mm CL) are recorded in the minimum size category.



lobsters. Similar data were collected in 1993 by experimental fishing during the closed season.

Stock dynamics

Spiny lobsters settle from their pelagic larval stage in shallow water and migrate to deeper water as they grow. Reproduction takes place on the fringing reefs at the edge of the bank. This migration pattern is reflected in the catches, where the size frequency is determined to a large extent by location (Fig. 1).

Lobsters landed at the start of the fishing season in August represent new recruits to the fishery and have a similar size frequency to lobsters from the shallow bank areas (Fig. 2). The average size in August is smaller than the rest of the season (Fig. 3) mainly due to the absence of larger lobsters. As the shallow-water areas exploited in August are depleted, many fishers disperse to deeper water fishing grounds where they catch larger lobsters (Fig. 1). Most recruitment to the fishery occurs during the closed season and there is a strong correlation between the catch taken in August and the total catch for the whole season (Fig. 4), patterns that are also observed in Cuba (Baisre and Cruz 1994). The correlation between the catch in August and the total catch reflects both the strength of the recruitment and the changes in fishing effort associated with expected earnings.

To improve understanding of the stock dynamics, it is necessary to develop a recruitment index based on the available catch and effort data. It would be possible to use the August catch to predict the total catch for each season as long as the fishery remains open access and there are no major changes in the socioeconomics. However, as effort controls are shortly to be introduced, an index is required that is independent of fishing effort and will lead to an improved understanding of the stock dynamics. Therefore, we developed a recruitment index based upon the estimated number of lobsters at the start of the season.

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Models

Catch per unit of effort (CPUE) declines rapidly from the beginning of the season, when it is at its highest. Given that almost all the catch in August are new recruits, an estimate of the initial population size derived from a model of the depletion at the beginning of the season can be used as an index of recruitment in that year. The model used to generate the recruitment index was a simple constant recruitment model (Allen 1966):

$$(1) \quad R_{i+1} = (R_i - C_i)e^{-M} + R_0(1 - e^{-M})$$

where R_i = population size of recruits at the beginning of day i, C_i = observed landings in numbers of lobsters on day i after the start of the season, and M = natural mortality/emigration (per day). The model does not distinguish between emigration and natural mortality, but makes these losses a constant proportion of the population size. The model assumes that without fishing, the population would be stable through the first month of the season with new arrivals ($R_0(1 - e^{-M})$) equal to the losses from mortality and emigration. The population size at the beginning of the season (R_0) can be used as an index of the abundance of recruits, being the number of recruits at the start of the season as well as related to the rate of their arrival.

A similar model can be used for the whole population, but in this case the number of recruits is allowed to vary:

$$(2) \quad N_{s+1} = (N_s - C_s)e^{-M} + \lambda I_{s+1}$$

where N_s = population size of all lobsters at the start of the fishing season s, C_s = total landings in numbers of lobsters in season s, and M = natural mortality (per year). The recruitment index (I_s) is the estimated initial population size of August recruits (R_0 in eq. 1) and is converted to total recruitment in numbers through an additional parameter (λ). Conversion to total recruitment is necessary because the August catch is limited to the area close to the fishing harbours and does not include either recruitment occurring later in the season or lobsters in shallow water refugia.

Method

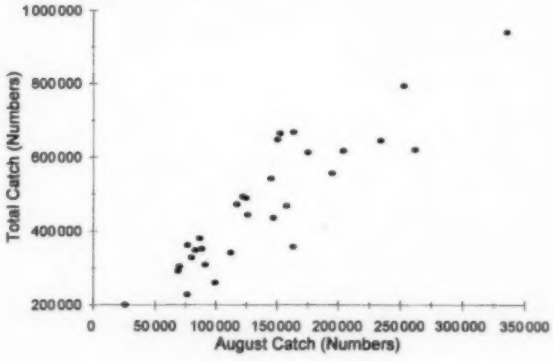
Fitting the models

The models were fitted to the observed catch and effort data by minimizing the Poisson deviance between the observed and expected catches (eq. 3), which produces maximum likelihood estimates. Empirically this is justified because the variance of the residuals was approximately proportional to the expected catch. However, there is also a theoretical justification for the Poisson likelihood. The mean catch would be expected to be equal to the variance if the fishers' search method and the distribution of lobsters were random (Poisson probability distribution). If the sample size was large, the normal distribution would be a reasonable approximation to this distribution, so least squares (the Normal deviance) would provide estimates close to the maximum likelihood. Although this is not unreasonable for the seasonal catch and effort data, where catches are large, for the small daily catches the Poisson deviance is more appropriate. It also assumes that catches less than zero are impossible, which should improve the estimates when expected catches are small. The equation is

$$(3) \quad E(x_t) = \mu_t = qf_tP_t$$

$$\text{minimize } D = 2\sum_{1}^{n}\left(x_t \ln\left(\frac{x_t}{\mu_t}\right) - (x_t - \mu_t)\right)$$

Fig. 4. Relationship between the catch for August and the total catch for the season.



where D is the Poisson deviance, μ_t is the expected catch in numbers of lobster, x_t and f_t are an observed catch and its associated effort, P_t is the population size calculated from the appropriate model (R_t for the recruitment index model and N_t for the population model), and q is the catchability. The subscript (t) refers to the position in the discrete time series, in days for the recruitment index model (eq. 1) and seasons for the population model (eq. 2).

Although the Poisson probability distribution arises naturally in counts, the underlying assumptions are rarely fulfilled and in this case the distribution is moderately overdispersed (variance > mean). Therefore, it is more appropriate to assume that the variance is proportional, rather than equal, to the mean, which was confirmed by examining the models' residuals. The parameters should still be maximum likelihood, but the overdispersed error will increase the standard error of the parameters above that expected of the Poisson distribution (McCullagh and Nelder 1983; Zeger and Qaqish 1988).

For the recruitment index model (eq. 1), a daily natural mortality and catchability parameter were estimated, as well as an initial population size parameter for each season. For the population model (eq. 2), four parameters needed to be estimated: catchability for the toss, catchability for the hook, natural mortality, and the recruitment index conversion factor. Separate catchability parameters for toss and hook were not included in the recruitment index model; it was not possible to fit two catchability parameters so that they only accounted for the change in the gear and not other changes in the time series.

Two sources of data were available. The recruitment index model was fitted to the daily catch and effort data for the first 31 days of the season for the periods 1977–1983 and 1986–1994. The population model was fitted to total seasonal catch and effort data over the periods 1977–1983 and 1986–1994, but also made use of reported catches extending back to 1966 and over the period 1984–1985 when effort was not recorded. The 1995 and 1996 seasons were reserved for testing model predictions. Trapping effort was excluded from the models, but trap catches were accounted for.

Estimating recruitment indices for years without effort data

Recruitment indices were unavailable for seasons prior to 1977 and for the 1984 and 1985 seasons. For these periods the index was estimated using a least-squares linear regression between the August catch and the recruitment index for available seasons. These estimates were necessary to provide continuity in the time series. In addition, estimating the index from August catches for years prior to 1977 avoided the necessity for estimating an initial population size for the annual time series model. The series of estimated indices and observed catches prior to 1977 make the 1977 population size largely independent of the initial population size for all reasonable initial population values. However, only those seasons with a true recruitment

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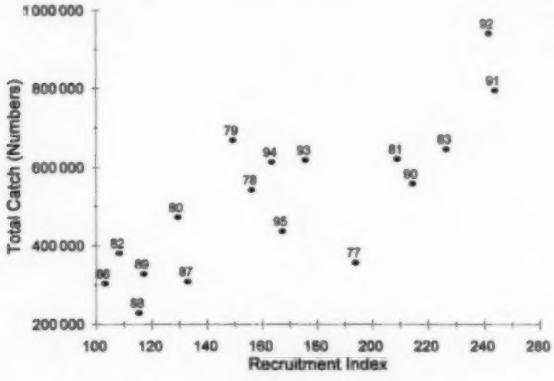
Fig. 5. Relationship between the recruitment index and the total catch for each season, 1977–1995. The pattern is similar to that shown between the August and total catch (Fig. 4). Note that in 1977 the season started in September and therefore was reduced in length by 1 month.



index were used in fitting the population model, which minimizes the effect of inaccuracies in the linear regression estimates.

Parameter reliability

It is not clear how reliable individual parameters are because of the complexities in the fitting process and the uncertain error distribution. In particular, it is unclear how the errors associated with the recruitment index will feed through to affect the final stock model. We investigated the parameter errors using a bootstrap technique (Efron and Gong 1983).

The following procedures were carried out for the recruitment index model (eq. 1). (1) A set of residuals was generated as the difference between the observed CPUE and expected CPUE derived from the maximum likelihood model. (2) A new CPUE datum was generated for each day by adding a new residual to the expected CPUE. Each new residual was drawn at random, independently with replacement, from the set of residuals in the same season. (3) The simulated catch was calculated as the new CPUE times effort observed on that day. (4) A complete set of simulated catches was used to refit the model to obtain a new set of bootstrap parameter estimates. (5) The linear regression was refitted between August catches and the bootstrap recruitment index estimates to obtain recruitment indices to complete the time series. (6) Procedures (2)–(5) were repeated 2000 times.

The bootstrap procedure was repeated for the population model (eq. 2). In this case, a new set of parameter estimates was obtained for each set of bootstrap recruitment indices. In all cases the simulated catches were only used to estimate observation error (eq. 3) and not used in the population models (eqs. 1 and 2) which continued with the real observed catches. The 2000 bootstrap estimates of all parameters were used to estimate the root mean squared error (√MSE), bias, and 95% confidence intervals for the parameters.

Results

The recruitment indices suggest that the main driving force behind fluctuations in catches and catch rates is recruitment ($R^2 = 0.942$, 425 df; Fig. 5; Table 1). Although the linear regression between the recruitment index and total August catches explained a significant proportion of the variance in recruitment index ($R^2 = 0.694$, 15 df, ANOVA, $P < 0.001$), the unexplained variation is still large. Estimates derived from the regression are unreliable and need to be treated with care. The stock model using the recruitment indices provides a good fit to the data ($R^2 = 0.984$, 12 df; Fig. 6; Table 2). It would appear that low recruitment was the main cause of the low catch rates during 1986–1989 and high recruitment for the subsequent recovery of the fishery. The seasonal natural mortality estimate is well within other published estimates for this species in the region (Baisre and Cruz 1994), and the model indicates correctly that the hook is more efficient than the toss.

The √MSE for all estimates was small relative to the size of the estimates themselves (Tables 1 and 2). In general the errors for the recruitment index increased with size and tended to be negatively biased. A fundamental problem is that the model does not fit all years equally well (Fig. 7) and is poor in those years with the larger bias (1979, 1983, 1988, 1991). The population dynamics for the recruitment index model should not be taken too literally. The constant recruitment assumption has probably been violated and it is likely that fishers have varied their behaviour from season to season which would also affect the estimates. However, the estimates are still valuable as recruitment indices even if they fail to estimate a true population size at the beginning of the season. Their ability to explain seasonal variation in the catches and catch rates is their greatest vindication.

The √MSE for the population model parameters was largely a result of the high correlation between parameter estimates. It is unlikely that errors will be greatly reduced, even with a longer time series, without estimating some of the parameters through other means. Surprisingly the √MSE suggests that the seasonal natural mortality estimate is relatively good. The greater uncertainty rests with the recruitment factor (λ) and catchability estimates. A few large values for these parameters appeared as a result of the relatively high errors and bias in the recruitment indices. Improving the recruitment index model and reducing the dependence on indices derived from the linear regression would reduce these errors significantly.

Stock–recruitment relationship

It is necessary to identify the appropriate lag between spawning and recruitment to develop a stock–recruitment relationship. There is no definitive growth model, but from the current understanding of the life history and growth of *P. argus*, a delay of approximately 3–4 years might be expected between eggs being released and recruits entering the fishery at 78–83 mm carapace length (CL) (Baisre and Cruz 1994; Briones and Lozano 1994). However, fecundity may continue to increase with age, which would be exhibited in the time series as a further delay between spawning and recruitment. Unfortunately, there is no direct measure of fecundity, as it is illegal to land berried females, and those that are landed have their eggs removed at sea.

As an alternative to a direct measurement of fecundity, we used the presence of the tar spot (spermatophore) on female lobsters as an indication of reproductive activity. The tar spot is easily identified and small enough not to interfere with catchability, but does not indicate how large egg masses are or how many are produced in a season. Tar spotting was analysed using a logit linear model, which is appropriate for binary data (McCullagh and Nelder 1983). As size-class sampling was not consistent through the year, it was necessary to use this model to separate the month and size effects.

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Table 1. Maximum likelihood and error estimates for the parameters of the recruitment index model.

Parameter	Estimate	√MSE	Bias	95% confidence interval	
M	4.82×10^{-2}	5.01×10^{-3}	5.88×10^{-4}	3.84×10^{-2}	5.58×10^{-2}
q	1.19×10^{-3}	1.14×10^{-4}	2.40×10^{-5}	9.75×10^{-4}	1.41×10^{-3}
Seasonal R_0 (thousands)					
1977	194	13.6	–3.2	166	217
1978	156	10.8	0.9	137	179
1979	149	16.6	6.9	133	190
1980	130	11.2	–4.9	106	145
1981	209	14.3	0.0	181	237
1982	108	11.0	–3.9	85	127
1983	227	18.8	–7.0	187	255
1986	103	9.9	–0.2	85	123
1987	133	11.2	0.7	111	157
1988	115	11.8	–7.2	91	128
1989	117	10.6	0.5	99	140
1990	214	19.5	0.9	180	256
1991	244	19.7	–5.8	203	278
1992	242	17.3	–2.6	207	274
1993	176	14.5	4.9	155	208
1994	164	12.3	–0.5	141	188

Note: The daily catchability (q) and attrition (M) parameters were fitted to all seasons simultaneously. The attrition estimate is much too high to account just for mortality, and almost certainly includes emigration. The initial population size parameters (R_0) accounted for changes between seasons and the estimates were used as the recruitment index in the population model. The root mean squared error (√MSE) is calculated as the square root of the mean of the squared difference between the bootstrap estimates and the maximum likelihood estimate and bias as the difference between the maximum likelihood estimate and the mean bootstrap estimate, and the confidence intervals are the 0.025 and 0.975 percentiles of the bootstrap estimate distributions (Efron and Gong 1983).

The frequency of tar spots shows a clear pattern with month (ANOVA, $P < 0.001$; Fig. 8*a*) and size (ANOVA, $P < 0.001$; Fig. 8*b*). Reproductive activity is greatest during March–August, so that the estimate of spawning stock size should reflect the number of lobsters entering the closed season. The closed season was originally implemented to protect berried females, which also suggests that most spawning and egg release occurs at this time. The size-class frequencies indicate that the majority of the spawning stock would be female lobsters exceeding 103 mm CL. However, it is possible that newly recruited female lobsters (78–83 mm CL) would make some contribution to the number of eggs produced if they could from the recruited size to spawning size during the season (80% increase in body weight).

The annual population size estimates from the population model (eq. 2) were used to estimate the spawning stock size in each year. This was calculated as the mature lobsters entering the closed season:

$$(4) \quad S_s = (N_s - (1 - w)\lambda I_s)(1 - qf_s)$$

where S_s = the spawning stock size at the end of season s,

Fig. 6. Observed (circles) and expected (line) CPUE for spiny lobsters from the Caicos Bank. The expected CPUE was calculated from the population model (eq. 2) fitted to the catch and effort time series, 1977–1994. The 1995 and 1996 seasons show the available observed catch rates (circles) and model predictions based on the observed recruitment indices (line) and recruitment indices predicted from a stock–recruitment relationship (pluses) (see Fig. 9).

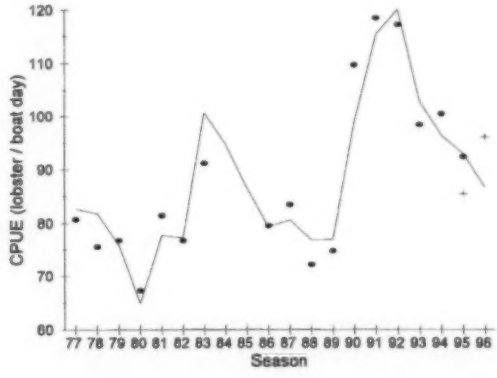

Table 2. Maximum likelihood and error estimates for parameters of the population model. Catchability for the toss refers to all seasons before 1982.

Parameter	Estimate	√MSE	Bias	95% confidence interval	
M	0.360	0.077	–0.007	0.214	0.514
λ	6.567	2.089	0.214	4.632	11.259
q (hook)	3.82×10^{-5}	9.69×10^{-6}	1.40×10^{-6}	2.08×10^{-5}	5.88×10^{-5}
q (toss)	3.11×10^{-5}	7.30×10^{-6}	4.27×10^{-7}	1.70×10^{-5}	4.62×10^{-5}

N_s = population size at the beginning of season s, λI_s = number of recruits, f_s = fishing effort, q = catchability for toss or hook as appropriate, and w = relative fecundity of new recruits as a proportion of mature lobsters. We initially assume that new recruits do not make a significant contribution to the spawning stock ($w = 0$).

The cross correlations between the estimated spawning stock size and the recruitment index time series (Table 3) suggest that a 4-year lag is appropriate, the linear correlation being very strong (Fig. 9). The linear relationship suggests no particular stock–recruitment model, and leaves open the question of what would be the major density-dependent controlling factor on abundance in the absence of fishing. A linear regression was used to predict the recruitment for 1995 and 1996 (Fig. 9). Although in both cases the observed recruitments are well within the 95% confidence intervals, using these projected recruitment indices reduces the seasonal model's accuracy (Fig. 6).

New recruits may make a contribution to the spawning stock, although their lower levels of reproductive activity implied by the tar spot analysis suggest that this would not affect the general results. Assuming some reasonable growth (one or two molts) during the season and that tar spot frequency (Fig. 8*b*) is a direct measure of fecundity, the fecundity of the new recruits would be 40–50% of the fully mature stock ($0.4 < w < 0.5$). This would be an overestimate, as fecundity, unlike

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Fig. 7. Observed (circles) and expected (lines) CPUE for August for two example seasons, 1978 and 1991. The expected CPUE was calculated from the recruitment model (eq. 1). The different time series for 1978 compared with 1991 illustrates the difficulty of using the same model to fit all seasons.

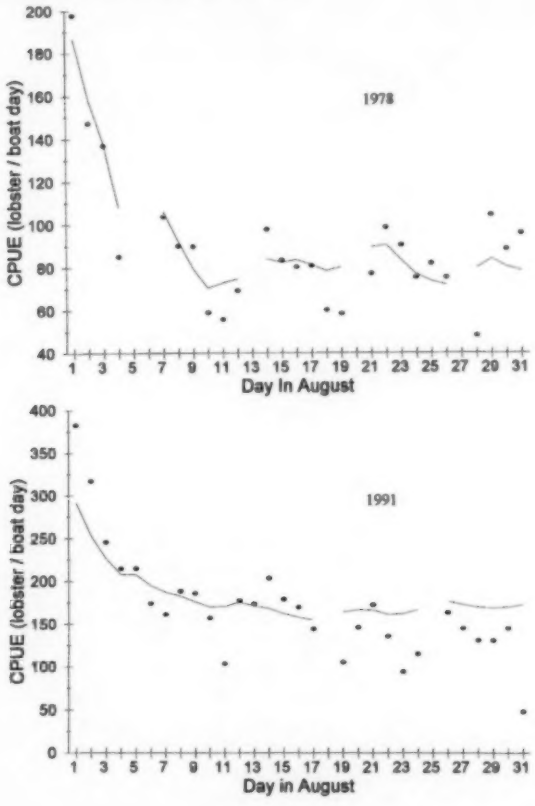
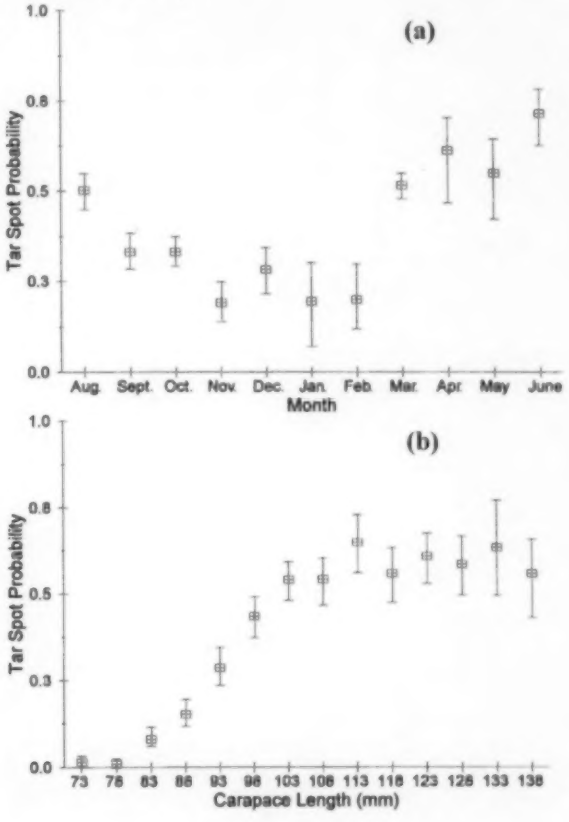


Fig. 8. Estimated tar spot frequency and 95% confidence intervals by (*a*) month and (*b*) size-class for female spiny lobsters. The estimates are calculated from a logit model which separates the month and size effects. For the month estimates, this can be interpreted as the probability that a female lobster will have a tar spot given that it has an equal chance of being drawn from each of the size-classes. Similarly, the size-class estimates assume that lobsters are drawn with an equal chance from each month. No data were available for July.



tar spot frequency, probably continues to increase with size beyond 103 mm CL. The underlying effect of increasing the fecundity of new recruits, thereby changing the way the spawning stock is calculated, is to gradually shift the observed lag between spawning and recruitment from 4 to 5 years. If recruit fecundity is less than 40% of the mature stock, the 4-year lag remains appropriate.

Discussion

The population dynamics model fits the annual time series data well, which is perhaps not surprising given the strong correlation between the August catch and the total season catch (Fig. 4). The form of the model is similar to that successfully used elsewhere (Phillips et al. 1994), although in this case, only catch and effort data are required. The model makes best use of the limited data in describing the observed population fluctuations. However, the final test is its ability to continue predicting future catches (Fig. 6), and its performance in this regard will be closely monitored.

The recruitment index model provides a good basis on which to assess the lobster stock. Without using a stock–recruitment relationship, the catches can still be accurately predicted up to the end of a season even if effort controls are implemented. In addition, management can set escapement levels of recruits to replenish mature populations by altering the length of the season, fishing effort controls, or catch quotas. Setting escapement levels would remain largely subjective in the absence of a stock–recruitment relationship, however, and would be based upon a general assessment of historical catch and recruitment data. Management would seek to enhance escapement to the brood stock in years when uncontrolled fishing mortality would be high, a factor that has probably contributed to long-term declines in catches in the past.

The proposed stock–recruitment relationship is less well supported. Although the pattern in the cross correlations is clear (Table 3) and the observed recruitment indices for 1995 and 1996 are well within the predicted confidence intervals (Fig. 9), there remain a number of problems. The short length of the time series and the lack of independent observations to support direct cause and effect make the relationship unreliable.

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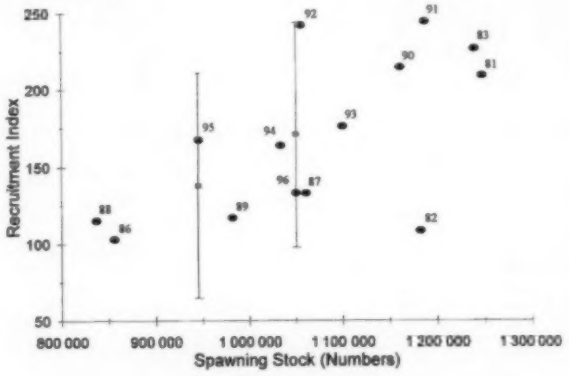
Table 3. Cross correlations between the estimated spawning stock size (S_s) and the recruitment index (I_s) at different lags.

Lag (seasons)	Correlation coefficient (r)
–6	0.34
–5	0.61
–4	0.72
–3	0.20
–2	–0.06
–1	–0.42
0	–0.37
1	–0.58
2	0.35
3	0.28
4	0.37
5	0.20

Note: Correlations with lags greater than zero are due to the direct effects of fishing and cohort growth, as recruits join the spawning stock. Negative lags can only be explained by external environmental factors or a stock–recruitment relationship.

Fig. 9. Relationship between recruitment and the estimated spawning stock size 4 years before. The point labels refer to the recruitment season. No reliable estimates of the spawning stock size exist for seasons before 1977, so recruitment seasons before 1981, which reference spawning stock sizes before 1977, are excluded. The recruitment indices for 1995 and 1996 have been predicted (boxes) with 95% confidence intervals using a least-squares linear regression for the seasons 1981–1994 excluding the outlier 1982.



Therefore the appropriate stock–recruitment model and the proposed lag remain tentative until supporting evidence becomes available.

A simple linear regression model between spawning stock and recruitment can only be adequate within the range of observations. Extrapolating the linear relationship would lead to an unstable population model if no density dependence is represented in the lobster's life history. Identifying and incorporating density dependence in the stock model will improve its accuracy and enhance its ability to predict future catch rates. It may also be possible to identify an optimum spawning stock size that management can target.

More observations are needed to improve the stock–recruitment model. It is possible that the 1982 season gives the first indication of density-dependent mortality, but it is also possible that this observation is a result of other anomalies such as unrecorded oceanographic effects, artifacts in the data, or management changes, such as the hook legalization in 1982. The only way to build up an adequate data set to develop the model further is to allow the spawning stock size to increase to the point that density dependence becomes apparent. Assuming the linear stock–recruitment relationship and using current parameter estimates (Table 2) in the spawning stock model (eq. 4), the spawning stock size will increase indefinitely if effort remains below 5600 boat days. It has been proposed to limit the length of the open season to keep effort below this level, which should ultimately provide data to develop an improved model.

The 4-year lag evident in the cross correlations cannot be rejected on the basis of current growth and fecundity models. Estimates for the von Bertalanffy growth curve parameters from mark–recapture experiments suggest a time lag of 2.5–3 years (Baisre and Cruz 1994) if the growth curve is extrapolated from 83 mm CL back to settlement at 8 mm CL and 9–12 months is required for the pelagic larval stage. This rate of growth agrees with those obtained in laboratories over the same size increment (M. Pardee, unpublished data). However, the same information indicates that the growth rate in wild lobsters from 45 to 83 mm CL is half that achieved under laboratory conditions. This suggests that the von Bertalanffy growth curve probably overestimates the growth rate of lobsters immediately after settlement, and the growth curve cannot be extrapolated backwards. A longer postsettlement growth phase together with increasing fecundity with age could result in the 4-year lag observed.

Derivation of a robust stock–recruitment relationship is undoubtedly the most significant problem in modeling lobster population dynamics. The Caicos Bank lobster fishery offers a unique opportunity to further study such a relationship. Despite the inherent life history problems of *P. argus* with its extended pelagic larval period (Baisre and Cruz 1994), once recruited to the Caicos Bank the stock is essentially isolated and no adult immigration or emigration can occur. Further research is required to investigate the stock–recruitment relationship so that recruitment can be enhanced. As well as increasing the spawning stock size, management may be able to enhance recruitment through artificial means. The relatively high recruitments peaking in 1992 may be partly attributable to the casita programme, which placed around 400 artificial lobster shelters across the Caicos Bank, and may have increased the available lobster habitat (Eggleston et al. 1990, 1992).

The current results suggest that the stock is largely self-recruiting and the spawning stock requires careful management. This is a safer, more conservative approach than assuming that recruits arrive from elsewhere, since it will encourage better management of the local spawning stock. Evidence from population genetics studies suggesting a single panmitic spiny lobster population (Menzies and Kerrigan 1980; Lyons 1981) does not preclude the majority of recruits being derived from

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the local stock. The belief that lobsters may recruit from a wider region (Lyons 1981; Villegas et al. 1982) may lead to sustained poor management in countries that lack the political will to put their own house in order (Cobb and Phillips 1994). In the interests of improved management, we believe it should be assumed that the majority of recruits is derived locally unless proven otherwise. This study suggests that this assumption may turn out to be correct, at least for the Caicos Bank.

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DISCUSSION

Comment: Scientific inquiry and fish stock assessment in the Canadian Department of Fisheries and Oceans[1]

William G. Doubleday, D.B. Atkinson, and J. Baird

Introduction

Hutchings et al. (1997) claim that non-science influences can interfere with the dissemination of scientific information and the conduct of science in the Canadian Department of Fisheries and Oceans (DFO). To substantiate their claim, they quote from a number of documents published over a 10-year period. This comment responds to Hutchings et al. (1997) by describing the open system of peer review of stock assessments in DFO and by showing how misinterpretation and selective quotation gave a false impression of stock assessments of northern cod in the 1980s and 1990s and of the peer review process in DFO.

DFO peer review system for stock assessments

Hutchings et al. (1997) allude to deficiencies in the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) process yet fail to acknowledge that CAFSAC was replaced by a new stock assessment review process in 1993. DFO's fisheries science is conducted in a rigorous, transparent, and collaborative fashion. DFO's peer review system for stock assessment is among the most open in the world.

To obtain the information needed for analysis, DFO conducts research vessel surveys and monitors fisheries. Oceanographic and environmental information are also gathered. People outside DFO with relevant knowledge and information are brought into the process. For example, commercial fishermen conduct some mini-stock surveys and carry out Sentinel surveys in closed cod fisheries.

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[1] Comment on perspective by Hutchings et al. 1997. Can. J. Fish. Aquat. Sci. **54**: 1198–1210.

A multidisciplinary teamwork approach is basic to DFO stock assessments. Data are analyzed by teams with members drawn from DFO and outside. Stock assessments are reviewed in meetings of scientists and fishers. These meetings include university-based scientists and fishers knowledgeable of the stocks. These participants from outside DFO see all of the data, analyses, and results. Once discussion is complete, stock status reports are completed, reflecting the results of the peer review. The text of these documents is reviewed and agreed upon as part of the peer review process. Stock status reports receive final editing at the Canadian Stock Assessment Secretariat.

Working papers are revised to reflect the discussions and are then made publicly available as research documents. Proceedings of the assessment meetings are produced. These proceedings reflect the differing opinions put forward during the meetings. Reasons for accepting or rejecting different analyses are included. These proceedings are available to the public.

External participants in peer review meetings know the results of stock assessments before DFO managers or the Minister of Fisheries and Oceans. Such an open system is not vulnerable to the kind of tampering that Hutchings et al. (1997) claim is occurring.

In the case of Atlantic groundfish, DFO's stock status reports are made public and are provided to the Fisheries Resource Conservation Council (FRCC). This arm's-length body is composed of individuals experienced in the fishery and university-based scientists, together with ex-officio members from provincial governments and DFO. The FRCC reviews scientific information from DFO and consults publicly across Atlantic Canada and Quebec before recommending conservation measures to the Minister of Fisheries and Oceans. A similar council for the Pacific has been initiated via a Canada – British Columbia agreement and is planned to begin operations in early 1998.

1986 CAFSAC review of northern cod

Hutchings et al. (1997, p. 1201) criticize the way that CAFSAC Advisory Document 86/25 (CAFSAC 1986) deals with uncertainty while lauding a working paper by Winters (1986). They draw particular attention to "a statistically significant negative association between inshore catch rate and offshore exploitation rate." This correlation was calculated with data for 1981 excluded because of an inshore fishermen's strike. As was

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pointed out in the peer review meeting at the time, there was no inshore fishermen's strike in 1981. It occurred in 1980 (Union Forum 1981). When the 1981 point is included in the analysis, the correlation is no longer statistically significant. This is not "an excellent example of the incompatibility of government bureaucracy and normal scientific inquiry," as Hutchings et al. (1997) proclaim, but rather a case of an error that was detected in peer review. Other parts of Winters' working paper were reflected in the CAFSAC advice (e.g., p. 5).

Was it normal to quantify uncertainties in stock assessments in 1986? Not at all. NOAA (1986), which contains scientific advice on fishery resources off the northeastern United States, presents point estimates of parameters such as stock biomass and fishing moralities without confidence intervals. The same is true for the northeast Atlantic (ICES 1986). Presenting confidence limits in stock status reports is a practice of the 1990s. Restrepo et al. (1992), a group of U.S. scientists and DFO scientists, using the same data available to CAFSAC in 1990, carried out a comprehensive risk assessment that suggested, based on the 1990 data, that the probability of the 1991 fishing mortality on northern cod exceeding the 1990 value was less than 0.05 (Fig. 2, p. 739), if the 1991 catch did not exceed 190 000 t.

Alverson

Hutchings et al. (1997) quote selectively from the independent review by Alverson et al. (1987). What Alverson et al. (1987) said about the growth of the stock was

> "Estimates of the growth of the stock may have been overly optimistic, and although we conclude that the total stock has increased since 1977, it has not reached the expected levels. Nevertheless it currently appears to be increasing, but at a slow rate" (pp. 1–2).

Alverson et al. (1987) estimated a 5-fold increase in stock size between 1976 and 1986, whereas CAFSAC scientists had estimated a 5.5-fold increase over the same period (Lear and Parsons 1993). This means that they did not agree with the Keats report (Keats et al. 1986), which they had received and which Hutchings et al. (1997) argue DFO was remiss in treating. What Alverson et al. (1987) said about fishing mortality was

> "The assessment methodologies employed by the fishery center at St. John's should lead to reasonably accurate estimates of stock abundance. The CAFSAC estimates of fishing mortality in 1986 fall within the (0.2–0.4) range of estimates supported by the data, but at the lower end of the range accepted by the Task Group and estimates made between 1976 and 1986 proved to be too low. Our selection of VPA methodology which leads to a less optimistic growth of the stock(s) reflects (*i*) our concern over the NAFO consistent underestimation of F, and (*ii*) our judgement as to the methodology which is not only consistent with available data but which takes into account the underlying uncertainties and risk associated with such estimates" (p. 3).

The independent Task Group introduced methods of calibrating VPA not previously used for northern cod, leading to different and, judged in retrospect, better estimates. The Task Group made no mention of any "bureaucratic influence" or any other conjecture to explain why their estimates differed from those of CAFSAC. Better methods give better estimates.

Harris

Hutchings et al. (1997) make no mention of the *Independent review of the state of the northern cod stock* (Harris 1990). This review was commissioned by the Minister of Fisheries and Oceans after CAFSAC provided substantially reduced estimates of the abundance of northern cod in 1989. The omission is unfortunate because Harris (1990) puts in perspective the assessments of the mid-1980s. As noted by Hutchings et al. (1997), the research vessel survey for groundfish in Divisions 2J + 3KL increased dramatically in 1986 over 1985. The 1986 survey was completed in the late fall and was used in the following year's assessment. The high survey value in 1986 was seen as corroborating the increasing offshore commercial catch rates and confirming the stock estimates from use of commercial catch rates. This changed when the 1987 survey was sharply lower. In 1988, estimates based on the survey could not be reconciled with estimates based on commercial catch rates, which continued to increase. CAFSAC delayed their assessment until January 1989 to use the results of the 1988 fall survey. Once the 1988 survey data were available, it was clear that the commercial catch rates were not proportional to stock abundance and reliance was put on the research vessel series (Lear and Parsons 1993).

What did the Independent Review say about the 1989 CAFSAC assessment?

> "... we accept the current CAFSAC estimate of fishing mortality at 0.44 as being most probably in the right domain" (p. 135).

The Independent Review adopted the CAFSAC assessment as a basis for catch projections. Contrary to popular recollection, Harris (1990) did not recommend closing the fishery. What he recommended was that

> "there should be an immediate reduction of fishing mortality to the level of at least 0.3 and, at the earliest feasible date to the level 0.2" (p. 151).

1992 projection of northern cod

Hutchings et al. (1997) criticize a projection of spawning stock biomass included in the 1992 announcement of the moratorium on fishing northern cod (DFO 1992). The NAFO Scientific Council assessed northern cod in June 1992. Their assessment included estimates of the number of fish at each age in the population. The calculation that Hutchings et al. (1997) criticized was a straightforward projection of the peer-reviewed population estimates by NAFO. It is ironic that Hutchings et al. (1997) attack this projection. It assumed no fishing mortality because the fishery was closed and no increase in natural mortality, which Hutchings seems to be advocating in his papers, including the May perspective article. Their reference to the intrinsic rate of increase, r, is illfounded because the projected increase of spawning biomass was due to the growth and maturation of the 1986 and 1987 year-classes already present (aged 6 and 5, respectively, in 1992) and estimated at the time to be quite strong. The lower values of the

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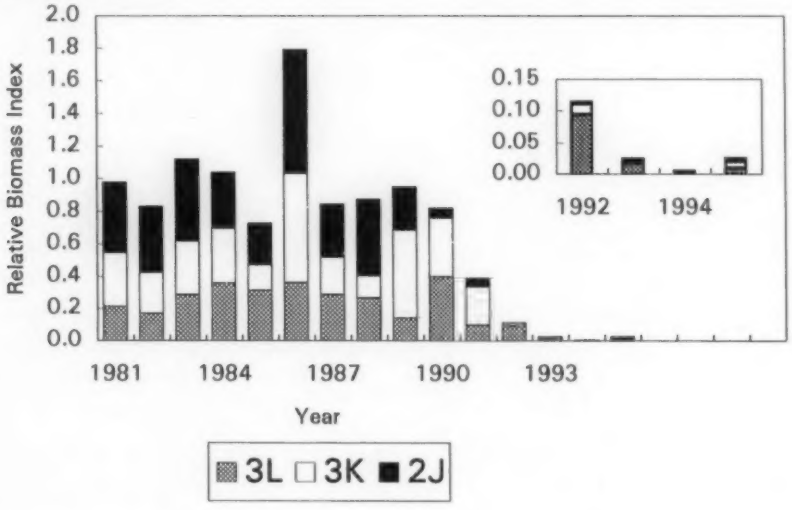
Fig. 1. Research vessel survey, northern cod.



parameter r quoted for cod generally reflect long-term averages.

In retrospect, it is clear that the spawning biomass did not increase as projected and as advised in the NAFO Scientific Council Report (NAFO 1992, p. 44). The fall research vessel survey, which is the main indicator of stock abundance used by DFO and others, continued to decline sharply in 1992, 1993, and 1994 (Fig. 1). The continuing rapid decline of the research vessel survey with apparent year-to-year total mortalities above 1.0 after the fishery closed suggests natural mortality was high in the early 1990s.

Media relations guidelines

DFO's Media Relations Guidelines[2] are similar to those of other government departments. The current guidelines state:

> "Public servants should be prepared to openly provide factual information to the public and the media within their areas of responsibility that describes or explains programs or policies that have been announced or implemented by the government. To contribute to open government, such interviews shall be on the record and for attribution. ... Public servants should not go beyond this discussion of factual information. ..."

DFO scientists have given hundreds of interviews over the past few years following these guidelines and with no prior approval by managers. To the best of our knowledge, no scientist in DFO has received a letter of reprimand for following these guidelines.

In addition, DFO has identified spokespersons to speak for the department on some issues. This is intended to avoid mixed messages and to ensure that spokespersons are familiar with the broad background of an issue and have the necessary skills to communicate clearly and effectively.

Hutchings et al. (1997) take issue with the letter of reprimand given to a DFO scientist for making the following statement in a Globe and Mail interview, August 25, 1995:

> "There are two messages in the research" said Department of Fisheries and Oceans research scientist Ransom Myers, who was the lead author of the study, "Decimated fish populations like the northern cod will recover if fishing is cut down ... and what happened to the (East coast) fish stocks had nothing to do with the environment, nothing to do with seals. It is simply overfishing."

The scientist attributed this to Myers et al. (1995). In fact, there is no such statement in this 1995 paper. To the extent that Myers et al. (1995) address environment and ecosystem effects on fish stocks, they take quite a different view. It states

> "The implication is that reductions in fishing mortality rates implemented by resource managers should enable currently remaining stocks to rebuild, unless environmental or ecosystem-level changes occur that alter the underlying dynamics of the stock" (p. 1108).

Significantly, Hutchings et al. (1997) justify the statement, not by referring to Myers et al. (1995), the subject of the August 25, 1995, interview with the Globe and Mail, but by reference to 14 other published papers, of which 10 were published in 1996 or later.

Elsewhere in their article (p. 1198), Hutchings et al. (1997) criticize DFO scientists for "failure to acknowledge fully scientific uncertainty and variability in scientific opinion." It is illogical for these authors to demand full acknowledgement of scientific uncertainty by departmental scientists and then to condemn the Department for pointing out to a scientist who makes a categorical and extreme statement that his statement did not give a balanced perspective and did not recognize the scientific uncertainties reflected in the regional stock status report. Hutchings et al. should realize that DFO's policy requiring objective, balanced statements must be implemented to be effective. They criticize statements that ignore uncertainty and variability in scientific opinion yet criticize the Department for asking a scientist to present a balanced view.

[2] DFO. Undated. Media relations guidelines. DFO, Communications Directorate, Ottawa, Ont.

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Stock status reports

Hutchings et al. (1997, p. 1997) claim that stock status reports by DFO are biased, in particular that the 1995 stock status report for Newfoundland Region (DFO 1995*a*) makes almost no mention of the potential influence of fishing on the groundfish collapse. The quotation is selective (part of one sentence) and misrepresents what the stock status report said. A more complete quotation shows that overfishing is given major attention in a balanced discussion.

> "**Ecological Perspectives**
> An important research activity is that of trying to relate all of the different observations described above; in other words to look at, and try to better understand the ecosystem. This is a difficult task, and we have a long way to go. However, based on our current information we can begin to see some similarities and differences, and begin to ask questions.
>
> For example, we may ask why so many of the "traditional" groundfish resources around Newfoundland declined at about the same time. For some of these such as the transboundary Grand Banks stocks of redfish (3LN), cod (3NO), yellowtail flounder (3LNO), witch flounder (3NO) and the southern component of 3LNO American plaice, the cause appears to be more related to overfishing, particularly on the young, immature sizes. The picture does not appear to be as clear for the other stocks. Both fishery and non-fishery causes have been put forward, and the relative importance of each may vary between stocks.
>
> For northern cod, there are differences of opinion. While some strongly advocate that the decline can be fully explained by fishing, others believe there was an important environmental component that must not be ignored."

Hutchings et al. (1997) also criticize the 1995 stock status report on Gulf of St. Lawrence groundfish (DFO 1995*b*), implying that seal predation rather than high fishing mortality was falsely being presented as the cause of the decline in southern Gulf cod. Here is what the report said about fishing mortality:

> "According to surveys, total mortality varied between 0.45 and 0.80 in the early 1970s to mid 1980s. There was a sharp increase in the late 1980s to levels greater than 1.0. The final estimate, which was for the 1990 to 1994 period, indicated a decline. This trend corresponds well with the trend in cod directed fishing effort and most likely reflects variations in mortality due to fishing" (p. 36).
>
> "Fishing mortality averaged approximately 0.6 up to 1988 (Figure 3.2.7) but then increased to around 1.0 in 1992. Fishing effort was reduced markedly in 1993 with the closure of the fishery. The catch of slightly above 5,000 t in 1993 resulted in a fishing mortality near the F0.1 = 0.2 reference level" (p. 37).
>
> "The current management system did not prevent the high level of fishing that was exerted on this stock in the 1989–92 period and the ensuing stock crash. Only one quarter of the historical fishing effort will be required to harvest the resource if it does recover. In the initial years of the recovery, fishing should occur well below this level. Reopening the fishery to the same fishing fleet and using the same management approach as before will likely result in immediate overfishing of the stock" (p. 38).

The stock status report for southern Gulf cod (DFO 1995*b*) does not mention seals at all and makes the above clear and strong statements about fishing mortality. How could Hutchings et al. (1997, p. 1203) conclude that seals are being blamed for the decline of southern Gulf cod? This is clearly a gross misunderstanding of the report.

The 1996 overview presentation on Atlantic groundfish (DFO 1996), which was shown to the Fisheries Resource Conservation Council in June 1996 and used in a video distributed across Atlantic Canada, was very clear about the reasons for the declines of Atlantic groundfish:

> "Contributing factors:
> - Domestic and Foreign overfishing
> - Poor fishing practices such as dumping and discarding
> - Unfavorable environmental conditions
> - Increased natural mortality"

This is the message communicated to the public; overfishing and poor fishing practices are the top two factors.

Kemano completion project

The events surrounding this matter are now a decade old and have been scrutinized through a number of mechanisms, perhaps most thoroughly through the eight months of technical hearings by the British Columbia Utilities Commission in 1993–1994 (BCUC 1994). Hutchings et al. (1997) quote selectively from documentation made public and provided to the Commission to build a case that DFO suppressed differing views of its scientists during the negotiation of a settlement of its court case. DFO provided over 100 000 pages of material from its files and encouraged any of its employees to testify before the inquiry. Opponents of the project were invited to name DFO witnesses that they wished to testify. All requested witnesses participated in the hearings. A wide range of views was expressed in the documents submitted and in the testimony of DFO employees. Hutchings et al. have been entirely one sided in their selection of testimony. The Commission's report was similar to, but more cautious than, the Settlement Agreement:

> "For the chinook and trout or the Nechako River, the Commission was not satisfied that the provisions of the Settlement Agreement were adequate, but was unable to set a precise estimate on the single level of flow that would be best." (BCUC 1994, p. *xxiii*)

The Commission concluded, with respect to the protection of fish and fish habitat, that to allow greater certainty, the program of habitat complexes should be replaced by somewhat greater flows and (or) hatchery operations. They then proposed three combinations of modestly higher flows, all less than existing flows provided under the 1987 settlement agreement, together with hatchery operations. They also concluded that the temperature used to trigger the release of cooling flows to protect migrating sockeye salmon should be decreased by 1 degree, from 19.4 to 18.4 degrees.

Summary

Contrary to the argument of Hutchings et al. (1997), DFO invited independent examination of the assessment of the northern cod stock and followed the advice of the *Independent*

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review of the state of the northern cod stock. Rather than suppressing information about the importance of high fishing mortalities in the decline of Atlantic groundfish, DFO stock status reports have highlighted its importance. DFO encouraged staff with a wide range of views to testify at the major BCUC inquiry. DFO's peer review system for stock assessments involves external reviewers who see the data and know the conclusions reached before DFO managers. We consider that the peer review process in place for Canadian fish stock assessments is as good or better than other systems in use elsewhere in the world.

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Comment: The interplay of policy, politics, and science[1]

M.C. Healey

Introduction

In their article, "Is scientific inquiry incompatible with government information control?", Hutchings et al. (1997) argue that political interference with science and the communication of science (specifically scientific uncertainty and scientific disagreement) in the Canadian Department of Fisheries and Oceans (DFO) has compromised DFO's efforts to sustain fish stocks. As examples they outline evidence of political manipulation of science to support political decisions in the collapse of Newfoundland's northern cod and the establishment of minimum in-stream flows for salmon conservation in B.C.'s Nechako River. As a solution they recommend the creation of a publicly financed but politically independent institution, like the former Fisheries Research Board, that would analyze the status of fish stocks and openly publicize the results. The article is a serious indictment of DFO but I believe that the authors' analysis is seriously flawed. Few would deny that the process of incorporating science into government decision making can be improved, or that the DFO bureaucracy sometimes makes bad decisions, or that ministers sometimes ignore scientific advice. However, in their criticism the authors display the same lack of objectivity and failure to assess the full range of alternatives of which they accuse DFO. My purpose in this comment is to offer an explanation, consistent with theories of public policy development and political agenda setting, for the interplay of politics and science in DFO and to show why an arm's-length scientific agency would not solve the problems with which Hutchings et al. (1997) were concerned.

Science in public policy

Since the Second World War, scientific advice has become a pervasive aspect of public decision making. Concern that scientific advice may be co-opted and distorted by policy makers (or, conversely, that scientists would co-opt the policy process) is not new (Jasanoff 1990). Because resource management has been characterized as a science-based activity, policies in resource management must be consistent with scientific evidence. Yet the fundamental decisions of resource management (e.g., what is an acceptable degree of restriction on harvest, who should be excluded from participation in the harvest, how should the harvest be allocated among participants?) are not resolvable by science. They are value judgments. In such a situation it is almost inevitable that objective and subjective judgments will become intertwined in decision making. That scientific credibility and political accountability are best served by strict separation of science and politics is a common argument (Jasanoff 1990; Hildreth 1994). Yet, in present-day Canadian fisheries management, the policy decisions of the minister must be backed up by scientific evidence if they are to carry any weight of authority.

Implicit in the arguments of Hutchings et al. (1997) is that the minister has an overriding obligation to conserve fish stocks. Although stock conservation is an important objective, it is by no means the minister's only concern and sometimes not even his/her primary concern. At times the minister may be more concerned with the economic well being of fishers or with Canada's fiduciary responsibility to First Nations, or another of the multitude of conflicting objectives that characterize fisheries management (Healey 1984). In any significant policy decision a wide variety of interests will compete for influence, and each interest will exploit scientific uncertainty and the diversity of scientific opinion to legitimize its preferred policy option (Wildavsky 1979; Wildavsky and Tenenbaum 1981; Healey and Hennessey 1994). The minister has to balance this conflicting advice with his/her own preferences and the advice of departmental officials in deciding on a policy. The increasing technical and scientific sophistication of competing interests in the fishery means that DFO scientists no longer have a monopoly on information and the techniques of stock assessment. Competing interests are all able to muster their own scientific and technical experts in support of their position.

In recent years the debate over policy alternatives has been very public. In the years preceding the collapse of northern cod and the Nechako Riverflow settlement agreement and in the aftermath, the public was presented with a bewildering range of scientific opinion and analysis of the issues. The decisions of the minister(s) of fisheries were scrutinized and criticized from every perspective and on the basis of comments by respected scientific authorities. In Newfoundland, there were three (four if one counts the Kirby report) commissions of inquiry into the status of northern cod before its collapse (Finlayson 1994) and there has been no shortage of public information, public scrutiny, and public debate since. In British Columbia, the implications of reduced flows in the Nechako River were subject to vigorous public debate before, during, and after the settlement agreement (BCUC 1994). Any interested member of the public must have been well informed about the alternatives and their putative scientific basis. In such situations it is easy to understand that the minister would seek

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[1] Comment on the perspective by Hutchings et al. 1997. Can. J. Fish. Aquat. Sci. **54**: 1198–1210.

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to bolster the authority of his policy decisions by (1) having a strong intramural scientific advisory team, (2) seeking advice on policy options and a consensus from the team, and (3) expecting that the team would respect the right and the responsibility of the minister to make the final decision among policy options.

The selection of a policy position is a highly political process, not a scientific one. A DFO scientist can remain aloof from this process (and many do) by providing scientific advice to the minister and senior bureaucrats and leaving the decisions about policy and the defense of policy up to the minister. If a scientist decides to enter the debate about policy, however, (s)he has to accept that (s)he has stepped out of science and into politics. If the scientist chooses to criticize the minister's position, (s)he has to expect that the minister won't like it.

Does this mean that science and the use of science in policy making by DFO are incompatible? I think the evidence is largely to the contrary. DFO science and DFO scientists enjoy an enviable international reputation for excellence. If the scientific corps of the Department did not exist, the minister would be compelled to create one simply because the public demands that fishery management decisions be scientifically credible. In almost all instances scientific advice from within the Department drives management decision making without much controversy. When controversy does arise it is usually because there is high scientific uncertainty and low predictability of the future (see, e.g., Wildavsky 1988); events preceding the collapse of northern cod and the Nechako River flow settlement agreement had these characteristics. In these circumstances, science has relatively little to offer and the minister may decide to go with his/her political instincts. Departmental scientists may find this situation frustrating but in the final analysis it is the minister, not the scientist, who is accountable to the public.

Value of an independent scientific organization

None of the foregoing denies the fact that ministers and senior bureaucrats sometimes make decisions that are not very credible scientifically, or that ministers and senior bureaucrats sometimes seek to interfere with the free pursuit of scientific understanding by Departmental scientists. Neither activity is in the interest of the Canadian public or, in the long run, in the interest of the minister and the Department. To address these kinds of failures in the relationship between science and policy development, Hutchings et al. (1997) propose an independent institution to conduct stock assessments. They do not provide many details about the structure and operation of this institution but say that it would be "...analogous to the Canadian judiciary" and that the former Fisheries Research Board "... may provide an appropriate model...." These are incompatible suggestions and because Hutchings et al. (1997) focus on the Fisheries Research Board and its precursors I will assume that is the kind of organization they prefer. There are a number of assumptions implicit and explicit in this proposal that, in my view, makes it untenable.

The first assumption is that an independent scientific organization would necessarily do the kinds of research and analysis that are needed for fisheries management decision making. In this context it is somewhat ironic that Hutchings et al. (1997) chose the Nechako River flow dispute as their example of political interference in science on the West Coast. In 1949–1950, the director of the Fisheries Research Board's Pacific Biological Station refused to assign his scientists to study the effect of damming and diverting the Nechako River on salmon in the upper Fraser. This refusal led the regional director of fisheries management to begin building his own in-house, biological analysis capability and created a rift between science and management that ultimately led to the dismantling of the Fisheries Research Board 20 years later. Publicly funded institutions that fail to serve the interests of the political system tend to be short lived (Healey and Hennessey 1994).

A second assumption is that science itself is without bias and uninfluenced by social and disciplinary fashion. That this assumption is false is obvious from even a casual reading of the literature on the history and evolution of scientific thinking (e.g., Finlayson 1994; Kuhn 1970; Gould 1981). The scientific perception of truth shifts and changes in response to social pressures, both internal and external to the discipline. Furthermore, at any particular time there are likely to be two or more scientific views of what is true competing for position and status within the scientific community. The kind of independent body that Hutchings et al. (1997) propose would not be immune to these forces and, thus, would be just one more scientific "voice" contributing to the debate.

A third assumption is that the public is unaware of scientific uncertainty and scientific controversy and that what they need is an independent organization telling them in detail the assumptions and implications of a range of policy options. On the contrary, it is my experience that the wider "public" is disinterested in the esoteric details of stock assessments and decision analysis. Furthermore, the public is bombarded with descriptions of the beneficial and negative consequences of policy alternatives by many competing interests. Public opinion appears to be dictated primarily by how the various policy alternatives correspond to widely accepted trans-scientific paradigms about the way the world works (Weinberg 1972; Healey and Hennessey 1994). Under the right circumstances the paradigm governing public opinion can go through a transformation but this is a socio-political process not a scientific one (Healey and Hennessey 1994).

A fourth assumption is that the minister would feel bound to accept the pronouncements of an independent scientific organization. A quick survey of the fate of recommendations from recent Royal Commissions (and commissions of inquiry into fisheries, e.g., Finlayson 1994) shows that politicians don't feel at all obliged to pay attention to the pronouncements of independent experts. Why, for example, would the analyses of an independent fisheries research organization have any more influence in the policy-making process than, say, the analyses of university faculty? The only way for such an organization to have significant influence in fisheries policy would be for it to align itself with one or more interests in the fishery and lobby for a preferred policy option. Then, however, the organization would have abandoned its scientific independence and taken on a political role. At that point, the credibility of the organization (and its budget) would be fair game for the minister.

A fifth assumption is that better data and analyses will necessarily lead to better policy. This is a belief that many

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scientists (and non-scientists) cherish but there is little evidence that it is true. In their analysis of the relationship between scientific information on oil reserves and energy policy in the U.S., Wildavsky and Tenenbaum (1981) showed clearly how intertwined were energy policy and estimates of oil and gas reserves. The authors argued that energy policy drove the estimation of oil and gas reserves as much as estimates of reserves drove energy policy. A similar argument can be made about fishery policy and stock assessments (Finlayson 1994).

Conclusions

Is scientific inquiry incompatible with government information control? In my opinion, the answer is no. Science is a critical component of effective social policy making and it is important that the minister of fisheries should have access to high quality scientific advice. However, in the complex multifaceted activity that is fisheries management, scientific information on fish stocks is not the only important consideration. Nevertheless, ministers who ignore science to the detriment of fish stocks are accountable to the public. Scientific experts are not.

Would the creation of an independent scientific organization to conduct stock assessments and analyze policy options improve public understanding and increase ministerial accountability? I very much doubt it. This is not to say that there would not be long-term benefits to Canada and the world if science were better supported in Canada and if there were more options for young scientists to pursue a career. Among industrialized countries, Canada has an abysmal record of expenditure on science and technology. However, for the reasons noted above, an independent science organization for stock assessment would not eliminate the manipulation of government science in support of ministerial policy decisions.

Can the relationship between fishery science and fishery policy development be made more effective? In my view, there are a variety of institutional reforms that would help. Firstly, both policy makers and scientists could take responsibility for developing a greater understanding of the others' needs and limitations (see e.g., Aquatic Science Evaluation Committee 1995). This would provide a better basis for communication and reduce the frustration of unfulfilled expectations between scientists and policy makers. Secondly, DFO could make a greater effort to treat policy initiatives as experiments in a program of adaptive assessment and management (Walters 1986; Lee 1993; Healey and Hennessey 1994). This would ensure that useful information derived from policy initiatives, particularly in instances where knowledge and predictability are weak. Thirdly, fisheries scientists could begin studying fisheries as complete systems rather than as disaggregated, discipline specific bits. Such an approach would allow for a more meaningful assessment of the importance of stock conservation in the context of the social and economic pressures that often drive decisions about policy (e.g., Ludwig et al. 1993).

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Reply: Scientific inquiry and fish stock assessment in the Canadian Department of Fisheries and Oceans[1]
and
Reply: The interplay of policy, politics, and science[2]

Jeffrey A. Hutchings, Richard L. Haedrich, and Carl Walters

The collapse of Atlantic cod was the unifying theme of Memorial University's EcoResearch project "Sustainability in a cold ocean coastal environment." The project entailed a broad-scale examination of the history, context, and consequences of that collapse. One objective was to analyze the role of science in fishery management decisions. The research question that became the title of our paper (Hutchings et al. 1997) was developed within that framework. We concluded that an environment in which information can be controlled, for whatever reason, is not one in which the scientific process can exercise its full potential. Our attention was drawn to the institutional structure that results in such an environment. After identifying what we perceived to be undesirable consequences of having science fully integrated within government, we posed the question, how should the structure be changed?

Doubleday et al.'s (1997) comment is a welcome contribution to this examination. They make the valid point that the present stock assessment review process is more open to non-DFO employees than in the past. However, they charge that by misinterpreting and selectively quoting from Department of Fisheries and Oceans (DFO) documents, Hutchings et al. (1997) "give a false impression of stock assessments of Northern cod in the 1980s and 1990s." Because of our comparatively minor treatment of northern cod stock assessments, Doubleday et al.'s point of departure is surprising and draws attention away from the main points of our perspective. We examined neither the structure of stock assessment models nor their ability to estimate stock size and fishing mortality, rendering superfluous the discussion of the Alverson and Harris reports by Doubleday et al.

Doubleday et al. (1997) describe the stock assessment review process presently used by the DFO. We agree that the recently modified system has many desirable aspects. For example, the presence of fishers and non-DFO scientists at assessment meetings has been viewed in a positive light by all parties. However, the integration of outsiders in the assessment process is not nearly as complete as Doubleday et al. imply. First, assessment documents are not written in a form readily accessible to non-scientists. Second, in Atlantic Canada, involvement of non-DFO scientists can range from a full review of assessment documents received prior to assessment meetings (a good practice) to a simple response to general open invitations to attend meetings and provide comment (a considerably less effective practice). However, involvement by non-DFO employees in actual stock assessment data analysis, i.e., running and tuning Virtual Population Analyses (VPAs), is rare, if it occurs at all. Thus, in practice, the production of, and the ability to comprehensively review, stock assessment documents remains a DFO "in house" affair in many important respects.

Doubleday et al. (1997) appear to have misunderstood our discussion of scientific concerns regarding northern cod in 1986. We focused on the convergence of conclusions among DFO and non-DFO scientists regarding both the overestimation of northern cod biomass and the underestimation of fishing mortality on this stock. We cited Winters (1986) because of the many uncertainties that he identified. Although scientific uncertainty with respect to stock size and fishing mortality prompted several recommendations by CAFSAC at the time, it was not until 1989 that these uncertainties were reflected by somewhat reduced catch quotas. Doubleday et al. (1997) do not explain why these significant recommendations were not enacted within the time frame specified by CAFSAC.

Regarding the projected increases in northern cod spawning stock biomass between 1992 and 1994 (Doubleday et al. 1997), these were based on numbers-at-age estimates from VPA. Uncertainties in these numerical estimates were not quantified. In addition, the projections did not account for the well-known "retrospective" problem associated with VPA numerical estimates (Smith and Gavaris 1993; Myers and Cadigan

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[1] Reply to comment by Doubleday et al. 1997. Can. J. Fish. Aquat. Sci. **54**: 1422–1426.
[2] Reply to comment by M.C. Healey 1997. Can. J. Fish. Aquat. Sci. **54**: 1427–1429.

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1995), namely that statistical biases in the estimation procedure cause abundances of current cohorts to be consistently overestimated. Regarding their Fig. 1, again we note the absence of simple uncertainty measures, e.g., standard errors, an omission apparently consistent with the reporting of point estimates in stock assessments in the 1980s (Doubleday et al. 1997).

Concerning the reprimand of a DFO scientist, this was justified by Doubleday et al. (1997) by reference to DFO's Media Relations Guidelines. Such reprimands may be acceptable in a tightly managed bureaucracy, but from a scientific perspective, we believe it is unwarranted for a DFO scientist to be disciplined for publicly stating the conclusions of peer-reviewed published research, irrespective of the reason for which a scientist is interviewed by the media.

Doubleday et al. (1997) do not address our criticism that the 1995 Newfoundland and Gulf of St. Lawrence groundfish stock status reports (SSRs) inadequately reflected the breadth of scientific interpretation of available data. Despite the existence of at least six relevant papers, evidence that fishing was the primary cause of the decline of northern cod was excluded from the 1995 Newfoundland SSR, with the single reference to fishing appearing under the heading "Ecological Perspectives." Further to our point that SSRs that discuss stock collapses should "identify all relevant scientific documents upon which this research is based" (Hutchings et al. 1997, p. 1202), we note that the scientific information in the Newfoundland SSR quoted by Doubleday et al. (1997) is not supported by any of the four documents cited at the end of the SSR's overview. That SSRs are public documents does not negate Departmental responsibility to fully document interpretations of scientific data, especially when one considers that SSRs comprise the primary scientific source for the Fisheries Resource Conservation Council, the non-scientific body that now makes Atlantic groundfishery recommendations to the Minister. All SSRs must be approved by senior Departmental officials before public release, one of several important points in our perspective not addressed by Doubleday et al. (1997). The existence of such an information filter, irrespective of the frequency and the strength with which it is applied, is incompatible with Doubleday et al.'s (1997) laudable objective of increasing the openness of stock assessment reviews.

Regarding the 1995 Gulf of St. Lawrence groundfish SSR, we neither implied nor concluded that "seals are being blamed for the decline of southern Gulf cod" (Doubleday et al. 1997). Our point was that scientific conclusions regarding the influence of seals and the physical environment on the decline of a cod stock were removed from the SSR, contrary to the advice of scientists who conducted the stock assessments (Hutchings et al. 1997). Occurring *after* stock assessment peer review, we argued that this type of intervention was inappropriate, counter to scientific understanding of biological phenomena, and inconsistent with the objective of full public disclosure of scientific interpretations of stock assessment and research survey data.

In a separate comment, Healey (1997*a*) argues that our analysis is seriously flawed and that we lack objectivity, but he provides no justification for these opinions. He also notes that science is only one of several factors upon which management and policy decisions are based. This obvious statement strengthens rather than diminishes our assertion that the scientific information presented to the Minister should be divorced from nonscience influences and that the scientific basis and ramifications of all management decisions should be made explicit and public. We concur wholeheartedly with Healey's (1997*a*) praise of the high quality of DFO science. However, we disagree that "science has relatively little to offer" in those situations for which there is high uncertainty. On the contrary, it is on such occasions that science has potentially the most to offer. Risk analysis, for example, permits many uncertainties to be quantified, thereby providing resource managers with a means of assessing the potential biological consequences associated with various management options.

Healey (1997*a*) agrees with us that "ministers and senior bureaucrats sometimes make decisions that are not very credible scientifically...and...sometimes seek to interfere with the free pursuit of scientific understanding by Departmental scientists," but he disagrees that greater independence of science from government would reduce the incidence of such decisions and interference. First, we note that with the exception of the first assumption mentioned in his discussion of scientific independence, the assumptions are Healey's (1997*a*), not ours. Second, his arguments here against the formation of an independent scientific body appear to be inconsistent with his recommendation elsewhere for "an independent auditor for the state of our [Pacific salmon] fishery resources...capable of reviewing the technical information on the state of fish stocks and making public comment on the resource" (Healey 1997*b*).

Our perspective ended with the suggestion that a reorganization of the link between scientific research and management of natural resources merited serious and open debate. The comments by Doubleday et al. (1997) and Healey (1997*a*) represent preliminary forays into such a discussion, and as such we welcome them.

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   Gretzky*, W., and J. Villeneuve. Department of Epidemiology, Eastern University, Yoho, Saskatchewan.

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